University of Sussex

LASI
LABORATORY OF APICULTURE AND SOCIAL INSECTS

Helping the Honey Bee and Other Flower-Visiting Insects in Urban Areas

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December, 2014

Submitted for the degree of Doctor of Philosophy

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Declaration

I hereby declare that this thesis has not been and will not be submitted in whole or in part to another University for the award of any other degree. However, the thesis incorporates to the extent indicated below, material already submitted as part of required coursework for the degree of:

Andy Madsen

In: BSc (Hons) Ecology & Conservation,

which was awarded by the University of Sussex in 2012.

Andy Madsen performed the experiment and wrote the final-year project dissertation using the data collected on borage (*Borago officinalis*), which later formed part of the extended dataset used in Chapter 4 of this thesis.

I certify that, with the above qualification, the work carried out in this thesis is entirely my own, and that any help provided by other individuals with data collection and analysis is fully acknowledged.

Signature: .....

Mihail Garbuzov

UNIVERSITY OF SUSSEX

MIHAIL GARBUZOV, DOCTOR OF PHILOSOPHY

HELPING THE HONEY BEE AND OTHER FLOWER-VISITING INSECTS IN URBAN AREAS

SUMMARY

As is much of the world's biodiversity, bees and other flower-visiting insects are in global decline, largely due to human activities. The impacts of humans on wildlife can be ameliorated, at least to an extent, by wildlife-friendly management practices in both rural and urban areas. This thesis comprises two introductory chapters (Part 1), followed by a series of ten research chapters (Parts 2 - 5) aimed at informing management practices that encourage bees and other flower-visiting insects in urban areas, and ends with a concluding chapter (Part 6). The projects are grouped in four parts making contributions to four broad areas of research. Part 2 is concerned with evaluating the attractiveness of ornamental garden plants to insect flower-visitors. Individual projects examine the advice currently available to gardeners via recommended plant lists, and describe surveys of plant varieties grown in a public garden (Southover Grange garden, Lewes), a Plant Heritage national collection of asters (Picton Garden, Malvern), and the experimental gardens planted on campus of the University of Sussex, Brighton, as well as in towns of Plumpton and Magham Down. Part 3 evaluates the attractiveness to insects of urban wild flowers, including those growing in amenity grass areas in parks, and the effects on their abundance and diversity of the various mowing regimes, as well as the attractiveness of the common autumn flowering ivy. Part 4 uses waggle dance decoding to investigate honey bee foraging in the urban landscape of Brighton, with an additional particular focus on foraging on spring-blooming oilseed rape in the surrounding agricultural land. Part 5 examines an aspect of good practice in urban apiary set up, the use of lattice fence or hedge barriers, which should facilitate beekeeping in urban areas, including in private gardens and allotments.

Publications arising from this thesis

Published or accepted for publication/in press

Garbuzov, M., Ratnieks, F.L.W. (2014) Listmania: the strengths and weaknesses of lists of garden plants recommended to help bees, butterflies and other pollinators. *BioScience*, **64:** 1019-1026. (Chapter 3)

Garbuzov, M., Ratnieks, F.L.W. (2014) Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects. *Functional Ecology*, **28:** 364–374. (Chapter 5)

Garbuzov, M., Samuelson, E.E.W., Ratnieks, F.L.W. (In press) Survey of insect visitation of ornamental flowers in Southover Grange garden, Lewes, UK. *Insect Science*, doi: 10.1111/1744-7917.12162 (Chapter 6)

Garbuzov, M., Ratnieks, F.L.W. (2014) Ivy: an underappreciated key resource to flower-visiting insects in autumn. *Insect Conservation and Diversity*, **7:** 91-102. (Chapter 8)

Garbuzov, M., Fensome, K.A., Ratnieks, F.L.W. (In press) Public approval plus more wildlife: twin benefits of reduced mowing of amenity grass in a suburban public park in Saltdean, UK. *Insect Conservation and Diversity*, doi: 10.1111/icad.12085 (Chapter 9)

Garbuzov, M., Schürch, R., Ratnieks, F.L.W. (In press) Eating locally: dance decoding demonstrates that urban honey bees forage mainly in the surrounding urban area. *Urban Ecosystems*, doi: 10.1007/s11252-014-0403-y (Chapter 10)

Garbuzov, M., Ratnieks, F.L.W. (2014) Lattice fence and hedge barriers around an apiary increase honey bee flight height and decrease stings to people nearby. *Journal of Apicultural Research*, **53:** 67-74. (Chapter 12)

Submitted

Garbuzov, M., Madsen, A., Ratnieks, F.L.W. (Under review) No effect of patch size on insect visitation rate per unit area in garden-scale flower patches. (Chapter 4)

Garbuzov, M., Schürch, R., Couvillon, M.J.C., Ratnieks, F.L.W. (Accepted with revision) Honey bee colonies show limited foraging on oilseed rape, a potential source of neonicotinoid contamination. (Chapter 11)

Garbuzov, M., Ratnieks, F.L.W. (Submitted) Using the UK national collection of asters to compare the attractiveness of 228 varieties to flower-visiting insects. (Chapter 7)

Acknowledgements

It is my pleasure to express gratitude to many people that have helped me in completing this thesis. My biggest thanks, of course, goes to my supervisor – Francis Ratnieks, who provided a huge amount of input, including exciting ideas, stimulating discussions and manuscript comments, which were excellent examples of both critical and creative thinking to learn from. Francis also collected some data using experimental flower patches (Chapter 5) and ivy flowers (Chapter 8) in his own garden. I also much appreciated the way that Francis guided my work, which both enabled me to be productive and alleviated stress in difficult times.

My co-supervisor – Alan Stewart, was also very helpful in providing critical comments on the earlier manuscript drafts.

The help of Jodie Baker and Elizabeth Samuelson in decoding honey bee waggle dances (Chapters 10, 11) and making counts of flower-visiting insects (Chapter 5) has been invaluable. Elizabeth Samuelson also helped in making a survey of insects visiting flowers of ornamental plants being grown in the Southover Grange garden (Chapter 6), identification of oilseed rape pollen (Chapter 11) and scoring of ray floret colour in 228 varieties of aster (Chapter 7).

Ian Parkinson, David Lamb and their respective institutions – Wakehurst Place (part of Royal Botanic Gardens) and Plumpton College, provided permission and assistance in setting up experimental apiaries on their land, which were used to study the effects of barriers on honey bee flight height (Chapter 12). Plumpton College also allowed planting of an experimental flower bed consisting of 13 ornamental plant varieties (Chapter 5).

Richard Eborn of the Lewes District Council provided names of ornamental plant varieties being grown in the Southover Grange garden in 2012 (Chapter 6), most of which are impossible to identify down to the variety level in any other way, and so would have remained unidentified without his help.

Dan Danahar, Rob Sandercock and their institution – Dorothy Stringer School, have kindly allowed to place three honey bee observation hives inside the environment teaching building, which resulted in projects investigating honey bee foraging in the urban area of Brighton (Chapter 10), and particularly foraging on spring blooming oilseed rape in the nearby countryside (Chapter 11), as well as pollen foraging on autumn flowering ivy (Chapter 8).

Roger Schürch and Margaret Couvillon taught me how to use their novel methodology of incorporating inaccuracy in the waggle dance encoded vectors to quantify honey bee foraging in different types of landscape by means of their R script and the software ArcGIS, so that I was privileged to have used it before it appeared in the public domain (Schürch *et al.*, 2013). Margaret Couvillon has also collected waggle dance data from honey bee colonies located in the Laboratory of Apiculture & Social Insects (LASI) in 2011, which formed part of the whole dataset used to quantify spring foraging on oilseed rape (Chapter 11) in hives placed in two locations (LASI & Dorothy Stringer School) over two springs (2011 & 2012).

Katherine Fensome collected field data on flowers, flower-visiting insects and attitudes of park visitor towards the new grass mowing regime in the Saltdean Oval park as part of the project partially funded by the Brighton & Hove City Council to investigate the effects of reduced mowing on wildlife (Chapter 9). I am also grateful to Mark Gapper and Matthew Thomas of the council's CityParks department, who have contributed to planning of the study and were responsible for the creation and maintenance of the experimental sub-plots in the park.

Paul, Meriel and Helen Picton kindly allowed me to carry out a study of the attractiveness of 228 varieties of aster to flower-visiting insects in their national collection (Chapter 7) and provided much helpful advice and information, for which I am grateful.

Andy Madsen collected data on honey bee visits to experimental patches of borage (*Borago officinalis*) of different size, which was used in his final-year BSc project dissertation, and later formed part of Chapter 4.

Michael Schofield, a senior research technician at the School of Life Sciences, provided assistance in using the school's bright field microscope for the purpose of identification of ivy (Chapter 8) and oilseed rape (Chapter 11) pollen.

Luciano Scandian, a local beekeeper and the research apiarist at LASI has kindly loaned his own honey bee colonies for use in the experiment investigating the effects of barriers on honey bee flight height (Chapter 12). Luciano was also incredibly helpful with transport of colonies to and from both Wakehurst and Plumpton experimental apiaries.

Martyn Stenning was immensely helpful in many ways, from assistance in getting greenhouse space for growing plants to liaising with the university's estates department to obtain permission for planting experimental flower beds on the campus, as well as numerous small, but very important tasks, such as ordering equipment and materials from suppliers.

I am obliged to all members of the Laboratory of Apiculture & Social Insects, both past and present, in no particular order: Jelle van Zweden, Christoph Grüter, Margaret Couvillon, Roger Schürch, Martin Kärcher, Sam Jones, Tomer Czaczkes, Gianluigi Bigio, Karin Alton, Norman Carreck, Fiona Riddell-Pearce, Luciano Scandian, Hasan Al Toufailia, Tom Butterfield, Nick Balfour and Kyle Shackleton for interesting discussions, good advice, helpfulness, friendly atmosphere and useful comments on the early drafts of my manuscripts.

I am grateful to Dave Goulson and Ken Thompson for examining my thesis and providing interesting, constructive and useful comments.

Last, but not least, I would like to thank The Body Shop Foundation for providing funding, without which this thesis would not have been possible.

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Part 1: General Introduction and General Methods

Chapter 1

General Introduction

1.1 European honey bee – an important part of the thesis

Figure 1.1. Honey bee forager visiting flowers of garden catmint, *Nepeta x faassenii.*

The European honey bee (*Apis mellifera*, Fig. 1.1) is an important part of this thesis, with three chapters focused exclusively on its foraging behaviour (Chapters 10 & 11) and an aspect of beekeeping practice (Chapter 12), as well as a large part of Chapter 8 quantifying ivy pollen collection. The honey bee is one of about 250 bee species native to Britain (Baldock, 2008; Carreck, 2008). It is an obligately eusocial species, living in colonies with a reproductive queen and sterile female workers, and is the only species in Britain with perennial colonies that are, in principle, active throughout the year. Honey bees feed almost exclusively on nectar, which is the main source of carbohydrate, and pollen, the main source of protein, collected from flowers by foraging workers. The exceptions to this are 'honeydew' – a sugary excretion of aphids and some other sap-sucking insects (Moller & Tilley, 1989), and, very rarely, fungal spores, collected *in lieu* of pollen (Shaw, 1990).

Most honey bee colonies in the UK are managed by hobbyist or professional beekeepers. The colonies reproduce by swarming, whereby one queen with a group of workers leave the parent colony to found the daughter colony in a new nest (Seeley, 1985). Some swarms are captured by beekeepers, but others naturally nest in cavities, such as tree hollows. These newly founded colonies form the unmanaged, or wild, population. The extent or density of the wild honey bee population in the UK is unknown due to lack

of research, but some indirect estimates suggest that wild colonies are generally rare across Europe (Jaffé *et al.*, 2010). The wild population is also not genetically isolated from the managed population (Thompson *et al.*, 2014), as mating takes place in open air between drones and queens from hives up to 15 km apart (Jensen *et al.*, 2005).

1.1.1 Honey bee importance, declines and their causes

Honey bees are important producers of honey for human consumption, producing c. 1.6 million tonnes per year worldwide (FAO, 2011). However, their main economic importance is in the pollination of agricultural crops, valued at £230 million in the UK (Fig. 1.2, Mwebaze *et al.*, 2010) and $12 billion in the USA (Calderone, 2012). About three-quarters of the globally important food crops are to some extent dependent on animal pollination and the honey bee remains, by far, the most widely used species for this task worldwide (Klein *et al.*, 2007). The contributions of wild pollinators to crop pollination are also important (Garibaldi *et al.*, 2011; Garibaldi *et al.*, 2013) and it is possible that the value attributed to honey bees may have been overestimated (Breeze *et al.*, 2011).

Figure 1.2. Value of honey bees in pollination of UK agricultural crops: (a) apples, (b) oilseed rape, (c) raspberries, (d) strawberries, (e) field beans and (f) pears. Additional categories include mixed orchard fruits (£6 million) and other soft fruits (£6 million), not illustrated. Data from Mwebaze et al. (2010).

Although honey bee colony numbers are increasing worldwide, the demand for pollination services is increasing at an even greater rate (Aizen & Harder, 2009; Breeze *et al.*, 2014). Furthermore, declines on local, national and continental scales, such as those in Europe and USA, are a concern (Neumann & Carreck, 2010). Historical data indicate that the number of managed colonies in England and Wales has declined from approximately 1,000,000 in 1910 to 250,000 in 2006, i.e. a decline of 75% over the last century (Carreck, 2008). More recently, Potts *et al.* (2010b) estimated that the number of colonies in Europe declined by 16% between 1985 and 2005, which is largely due to the declines in central Europe (-25%) and Scandinavia (-14%), offset to a degree by the increase in Mediterranean countries (+13%). In the USA, average overwinter colony losses of c. 30% have been reported for the past several years (Steinhauer *et al.*, 2014), bringing ongoing difficulties to the beekeeping industry.

Multiple factors, acting alone, concurrently or synergistically could be responsible for these declines. The list includes the usual culprits, such as (i) habitat loss and land-use intensification, leading to the loss of available forage; (ii) pests and pathogens, including those specific to the honey bees (Genersch, 2010), (iii) pesticides, (iv) weather and climate, as well as (v) the socio-economic factors impacting beekeeping as a profession or as a hobby (vanEngelsdorp & Meixner, 2010; Smith *et al.*, 2013). Large-scale losses in the USA since 2006 were attributed mainly to the Colony Collapse Disorder (CCD), a term coined to describe a particular set of symptoms in the absence of a known cause, characterized by a rapid loss of adult worker bees and seemingly 'abandoned' brood and food stores (vanEngelsdorp *et al.*, 2009). While no one pest or pathogen has been identified as single a cause of the CCD, the general consensus appears that it is probably a result of a combination of stressors (vanEngelsdorp *et al.*, 2009; Ratnieks & Carreck, 2010), with viral diseases being most significant and the *Varroa* mites involved in their transmission (Francis *et al.*, 2013).

Despite the declines in colony numbers, the honey bee still remains a very common animal and is nowhere near the danger of extinction in the UK or elsewhere. Nonetheless, worrying downward trends, perhaps aided by attention-grabbing media headlines, have captured the public consciousness and led to the desire of many people to help (Spivak *et al.*, 2010). For example, the article by Bryan Walsh titled "*The Plight of the Honeybee*", which made it onto the cover of the *TIME* magazine (Fig. 1.3), paints a gloomy picture with a potential impending disaster for farmers and the supply of certain foods if honey bees continue to decline (Walsh, 2013). One way the public has been encouraged to help is to take up beekeeping as a hobby. However, as most people live in towns and cities, this often involves keeping the hives in back gardens or on rooftops. For example, many businesses in London, UK, have put up hives on their roofs as a means of appearing 'green' and showing off their pro-environmental agenda (Alton & Ratnieks, 2013). Indeed, in the 2008-13 period, the number of beekeepers in London tripled to 1,200 and the number of colonies doubled to 3,500 (Alton & Ratnieks, 2013). Chapter 12 reports a study of an aspect of good practice in urban beekeeping, showing that barriers can be used to reduce the number of stings to people nearby, such as neighbours or pedestrians. However, as the increase in hive numbers has not been accompanied by a corresponding increase in the abundance of flowers, a better way to help bees is to address this lack of forage (Alton & Ratnieks, 2013).

Figure 1.3. August 19, 2013, issue of the *TIME* magazine, with a cover featuring Bryan Walsh's article titled "The Plight of the Honeybee" that warns of a potential disaster for farmers in the case of a further honey bee decline. *TIME* has world's largest circulation for a weekly news magazine, reaching a very wide readership.

1.2 Declines of other flower-visiting insects

Data on other species of flower-visiting insects were collected as part of Chapters 3-9. Pollinators as a guild are in a state of global decline due to much the same causes (reviewed in Potts *et al.*, 2010a; Vanbergen & the Insect Pollinators Initiative, 2013). For example, declines in bumble bees in Europe over the past 60 years were driven primarily by habitat loss and intensification, resulting in lower abundance and diversity of flowers (Goulson *et al.*, 2008b). The abundance of wild bees, other than the honey bee, and hover flies (Diptera, family Syrphidae) declined in parallel with that of insect-pollinated plants in both Britain and the Netherlands since 1980 (Biesmeijer *et al.*, 2006). However, the rates of decline appear to have generally slowed down in native European pollinators since 1990, corresponding with, and maybe owing to the greater investment in conservation (Carvalheiro *et al.*, 2013). Given that the honey bee is a generalist forager (Crane, 1976), actions aimed at helping it by enhancing the availability of forage can, in principle, be also beneficial to other flower-visiting insects.

1.3 Conserving biodiversity and helping flower-visiting insects in urban areas

Traditionally, conservation measures have been focussed on natural (e.g. Forup et al., 2008), semi-natural (e.g. Tarrant et al., 2013) or agricultural land (Kleijn et al., 2006). However, attention has recently been extended towards urban areas (Miller & Hobbs, 2002; Sanderson & Huron, 2011). Urban and suburban areas cover 0.4% of the Earth's ice-free land area (Ellis et al., 2010) and, depending on definition, 6.8-9.5% in the UK (UK National Ecosystem Assessment, 2011), where the land use is otherwise dominated by agriculture (75%, DEFRA, 2012). In Britain, agriculture has become dramatically intensified since the end of WW2, which corresponded with, and probably caused, widespread declines in the abundance and distribution of many groups of organisms (Robinson & Sutherland, 2002; Fig. 1.4a). In this context, the potential role of urban areas

Figure 1.4. (a) Modern British landscape dominated by intensive agriculture, which is mostly used as grazing land, as well as the cultivation of arable crops: wheat, barley and oilseed rape. (b) Urban area of Hangleton district in Brighton & Hove, UK, showing a substantial proportion of green space.

in conservation is, arguably, no longer negligible. Dearborn and Kark (2010) suggest seven motivations for conserving urban biodiversity, which *inter alia* include ecosystem services, opportunities for public education and "citizen science", improvement of human wellbeing and, perhaps most importantly, the fact that, in some cases, urban areas can serve as important biodiversity reserves by supporting wildlife populations.

Urban areas, by definition, are heavily developed and it is not surprising that, in general, species richness of many groups of organisms tends to decrease with increasing levels of urbanization along rural-urban gradients (McKinney, 2008; Aronson *et al.*,

2014). However, as with all generalizations, there are exceptions that do not follow the overall pattern. In a review of 105 studies on the effects of urbanization on species richness, McKinney (2008) showed that about 65% of plant studies, 30% of invertebrate studies and 12% of vertebrate studies exhibit peak species richness at a moderate level of urbanization (i.e. suburban areas), consistent with the 'intermediate disturbance hypothesis', which predicts that, in many situations, species richness is highest at an intermediate level of disturbance and lower at both high and low levels of disturbance (Roxburgh *et al.*, 2004).

Urban areas contain many green spaces that can be a resource to wildlife, such as parks, gardens, lawns, road verges, cemeteries and brownfield sites (Fig. 1.3b). For example, Helden and Leather (2004) showed that urban roundabouts in Bracknell, UK, support rich and abundant Hemiptera communities. Green spaces also support flowers that present a forage resource for many flower-visiting insects. For example, Bates *et al.* (2011) found that, although the species richness of bees and hover flies and the abundance of bees decrease along a rural-urban gradient in Birmingham, UK, both these metrics are associated positively with the abundance of forb flowers. However, there were some notable exceptions: social bees that have relatively large foraging ranges, the honey bee (*A. mellifera*) and the red-tailed bumble bee (*B. lapidarius*), showed no negative response to urbanization (Bates *et al.*, 2011). Similarly, Ahrné *et al.* (2009) found that in Stockholm, Sweden, bumble bee abundance is positively related to local flower abundance, while species richness decreased with the proportion of built-up area, implying that responses to urbanization may vary among different bumble bee species. Some indirect evidence, based on parasite prevalence in workers, indicates that the buff-tailed bumble bee (*B. terrestris*) may even occur at higher densities in urban compared to rural areas (Goulson *et al.*, 2012). On a different continent, in New York City, USA, Matteson *et al.* (2013) showed that urban green spaces are associated with a higher abundance and species richness of flower-visiting insects then residential neighbourhoods, which was largely driven by the abundance of floral resources, vegetation type and cover. In and around Boston, USA, the abundance of blooming nectar-producing plants was found to

be an important determinant of butterfly diversity on a local scale, and the area of green space on a landscape scale (Clark *et al.*, 2007).

In an attempt to shed more light on the value of urban areas to honey bees, Chapter 10 investigates foraging by honey bee colonies located in Brighton, UK. The results revealed that urban colonies foraged mostly within the surrounding urban area throughout the season, despite the nearby countryside being well within their foraging range. This suggests that the urban area of Brighton can support honey bees year round, and corroborates the findings of Bates *et al.* (2011), who did not detect a decline in the number of honey bee foragers with increasing level of urbanization in Birmingham.

1.3.1 The value of gardens

In the mid-70s, Denis and Jennifer Owen recorded a rich diversity of insects in their suburban garden in the city of Leicester, UK (Owen & Owen, 1975). Their findings were at variance to the then prevailing view, which held that all man-made habitats, including gardens, were basically barren 'biological deserts'. The Owens were so impressed that it prompted them to suggest that suburban gardens, collectively, might be the "England's most important nature reserve" (Owen & Owen, 1975). The surveys carried on for 30 years and culminated in a book documenting 2673 plant and animal species recorded in this one garden, including 59 bees, 94 hover flies and 23 butterflies (Owen, 2010). However, this does not mean that all these species were living in this garden. Many, especially insects, were merely passing through and occasionally stopping to feed, such as butterflies feeding on floral nectar, which prompted Owen (1976) to compare gardens to 'refuelling stations'.

Indeed, of all types of urban green space, private domestic gardens, collectively, are probably the most important component in supporting urban biodiversity (reviewed in Goddard *et al.*, 2010). A survey of five major UK cities estimated that domestic gardens were 22-27% of the total city area, with an average area of 155-253 m^2 (Loram *et al.*, 2007). Nationally, 87% of UK households are associated with a garden, which constitutes an

enormous resource for wildlife (Davies *et al.*, 2009). Gardens in California, USA, (Frankie *et al.*, 2005; Frankie *et al.*, 2009) and even in the heavily developed neighbourhoods of the New York City (Matteson *et al.*, 2008) can support diverse bee assemblages. Recent studies showed positive effects of gardens on a landscape scale on both bumble bee (*B. lapidarius* and *B. pascuorum*) nest density and survival in the UK (Goulson *et al.*, 2010) and the abundance and richness of social and solitary wild bees in Sweden (Samnegård *et al.*, 2011). Additionally, indirect evidence based on the seed and fruit set of bee-pollinated plants implies that pollinator density may be enhanced by gardens on a landscape scale (Cussans *et al.*, 2010). Moreover, a UK-wide survey showed that bumble bee nest density within gardens is high and comparable to that in linear countryside habitats, such as fence lines and hedgerows (Osborne *et al.*, 2008a).

The value of gardens to wildlife can be enhanced by 'wildlife gardening'. That is, doing something to deliberately attract or encourage wildlife, such as feeding wild birds, having a compost heap, avoiding the use of chemicals or growing nectar-rich plants that provide food for flower-visiting insects (Good, 2000). A survey in England showed that most households with the use of a garden engage in some form of wildlife gardening (78%), which includes 66% that provide food for birds and 31% that select plants attractive to wildlife (Mew *et al.*, 2003). Motivations for wildlife-gardening are varied, but notably include personal wellbeing and a sense of moral responsibility for nature (Goddard *et al.*, 2013).

The UK garden flora is diverse and is characterized by a high proportion of alien species (c. ⅔) versus natives (c. ⅓) (Thompson *et al.*, 2003). Indeed, Gaston *et al.* (2007) have argued that gardening is inherently friendly to flower-visiting insects, as one of the things people are most keen to have in their gardens are flowers, whether they practice wildlife gardening or not. However, it is possible that some flowers, particularly ornamentals that were bred for their unusual appearance, such as by 'doubling' of petals, may be unattractive or inaccessible, and hence of little or no value to flower-visiting insects (Comba *et al.*, 1999b). In California, a team of researchers surveyed c. 1000 ornamental garden plant species and varieties over 5 years in two cities and found that

only 129 of them (or 13%) were attractive to bees to any measureable extent (Frankie *et al.*, 2005). Similarly, although on a smaller scale, Chapter 6 reports the results of a survey of 79 ornamental plant varieties in the Southover Grange garden – a public garden in Lewes, East Sussex, UK, showing that only a small proportion, 23%, were highly or moderately attractive to flower-visiting insects, while the remaining 77% were either poorly attractive or completely unattractive. These data suggest that there is a great scope for making urban gardens and parks considerably more valuable to flower-visiting insects by selecting and growing the right plants.

To help the public make informed choices, there are numerous lists of bee- and pollinator-friendly plant varieties, produced not only by amateurs (e.g. Creeser, 2004), but also by professional (e.g. RHS, 2011) and government organizations (e.g. Natural England, 2007). However, on closer inspection, some advice given in these lists is not particularly good. For example, Thompson (2006) described one list of wildlife-friendly plants produced by Natural England as "looks very much as if it was put together late one Friday afternoon". Chapter 3 makes a critical overview of a selection of such lists and finds that there is rather little overlap in their recommendations. Shortcomings include some poor recommendations, omission of many good plants, lack of detail, and the fact that almost all are based on their authors' general expertize, instead of empirical data. However, some recommendations given in lists are good, and, by virtue of being popular to the public, lists have merits in raising awareness and education. Chapter 5 attempts to put some of these recommendations on a firmer scientific footing by comparing 32 popular garden plant varieties in their attractiveness to insect-flower visitors. It finds that there is an enormous, approximately 100-fold, variation, suggesting that judicious plant selection by sympathetic gardeners can, in principle, make a big difference.

Chapter 2

General Methods

All research chapters (Chapters 3-12) have a section providing a detailed description of specific methods used. This chapter (Chapter 2) provides a broader overview and discussion of the general methods.

2.1 Studying foraging by quantifying insect visitation to flowers

The aim of several projects in this thesis (Chapters 4-7) was to compare the attractiveness of different plant varieties to bees and other flower-visiting insects. The main resource that insects obtain from flowers is food in the form of nectar and/or pollen, but plant species are hugely variable in flower size and the amount of resources they provide per flower. Thus, the variable that probably reflects the amount of floral resources gathered best is the amount of time an insect has spent foraging in a patch of flowers, rather than the number of individual flowers it visited. However, as it is obviously impractical to clock the time spent foraging by each individual insect, a proxy measure was used – the number of insects foraging in a patch of flowers in a near-instantaneous count or 'snapshot'. This count is directly proportional to the amount of time the insects spend, on average, in a flower patch, and is, therefore, a fair proxy of the amount of resources gathered and the benefit obtained by the insects from plants.

The relationship between an insect count and the amount of floral resources provided by the plants, which is of primary interest, is also affected by several co-variables. The most obvious co-variable is the area of a flower patch. One way to allow for this is to compare plant species or varieties grown in patches of the same area, as was done in Chapter 5, which compared 32 garden plant varieties, each grown in 1×1 m^2 patches. However, Chapter 4 specifically investigated the relationship between patch area and

count of foraging insects in a range of garden-scale flower patches (0.1 – 3.1 m^2) and found it to be linear. This result allows us to confidently compare plant varieties grown in patches of different areas, such as in gardens or parks, by expressing insect visitation as a count per unit area. In addition, patch area is a useful 'currency' from the perspective of gardeners or park managers, which can help relate the amount of benefit that flower-visiting insects may receive to the amount of land available for flower cultivation.

Another important co-variable is the flowering phenology, but it is more difficult to standardize among the plant species or varieties being compared. The amount of bloom was quantified by assigning it a score 0 (absence of bloom), 1 (< ⅓ of maximum), 2 (⅓ - ⅔ of maximum) or 3 (full bloom, > ⅔ of maximum) (after Anderson & Hubricht, 1940) and was accounted for by its inclusion as a term in models during statistical analyses. Chapters 5 & 6 compared garden plant varieties that are mainly summer-flowering and Chapter 7 compared *Aster* varieties that flower in the autumn. That is, the plants in each study flowered in the same general time period, even if not in complete synchrony. However, comparison of plants flowering at considerably different times, such as spring *vs.* autumn, would be heavily confounded by the time of season. The periods of time separated by a lengthy gap differ considerably in many respects, not least in weather, but also in phenologies and life cycle stages of plants, animals and other organisms, both under study and in the wider ecosystem, that there is no satisfactory way of accounting for all of these factors.

Insect activity itself is also affected by weather on a large scale and microclimate on a smaller scale (Corbet, 1990). For example, the minimum temperature permissive to foraging is lower in bumble bees, *B. terrestris/lucorum*, *B. pascuorum* and *B. hortorum*, c. 5 °C, than in the red-tailed bumble bee *B. lapidarius* and *A. mellifera*, c. 10-12 °C (Corbet *et al.*, 1993). However, within the narrower period of the flowering of ivy, *Hedera helix* and *H. hibernica*, in autumn, fluctuations in temperature between 14-24 °C had weak and often non-significant effects on the activity of flower-visiting insects (Chapter 8). But, to determine precisely the effects of weather and microclimate variables on insect foraging activity would require a whole study or a series of studies on their own. We have,

therefore, confined the insect counts to those periods, when, based on our experience, the weather was such as to allow all flower-visiting insect categories to be active.

It should also be noted that, due to the 'snapshot' counts being made, by definition, near-instantaneously (<10 s), the use of this method is practical only for relatively small patches (e.g. on a garden scale, up to c. 3 m^2) and with low to moderate numbers of insects per count (up to c. 10-15 individuals). However, larger patches could be studied in this way simply by sub-dividing them into manageable sub-units and summing the data.

2.2 Insect identification

Different species of flower-visiting insects have different flower preferences. It is, therefore, important not only to count the number of insects foraging in a patch of a certain plant variety, but also to identify them. The use of the 'snapshot' counts requires insects to be identified as they forage. That is, without capture for closer examination. This means that in many cases, an insect cannot be identified to species and so has to be identified to a higher taxonomic rank, such as a genus or a family.

2.2.1 Bees

According to the current systematics, bees belong to an unranked taxon Anthophila (meaning "flower lovers") within the superfamily Apoidea in the order Hymenoptera (Engel, 2005). Among the c. 250 bee species that occur in Britain, the honey bee, *A. mellifera*, is one of the few bees that is sufficiently characteristic to be identified to species on the wing. Others include the large and territorial wool-carder bee, *Anthidium manicatum* (Fig. 2.1a), common throughout England and Wales and the sole representative of the genus *Anthidium* in Britain (Pechuman, 1967), and the ivy bee, *Colletes hederae* (Fig. 2.1b), which, although very similar in appearance to other *Colletes*

spp., is the only one to be seen foraging on ivy in autumn due to emerging the latest in a season (Kuhlmann *et al.*, 2007). The identification of most other British bees (at least those encountered during fieldwork done as part of this thesis), even to the genus level, relies on microscopic characteristics, such as wing venation patterns, and is, therefore, not possible in the field (Baldock, 2008).

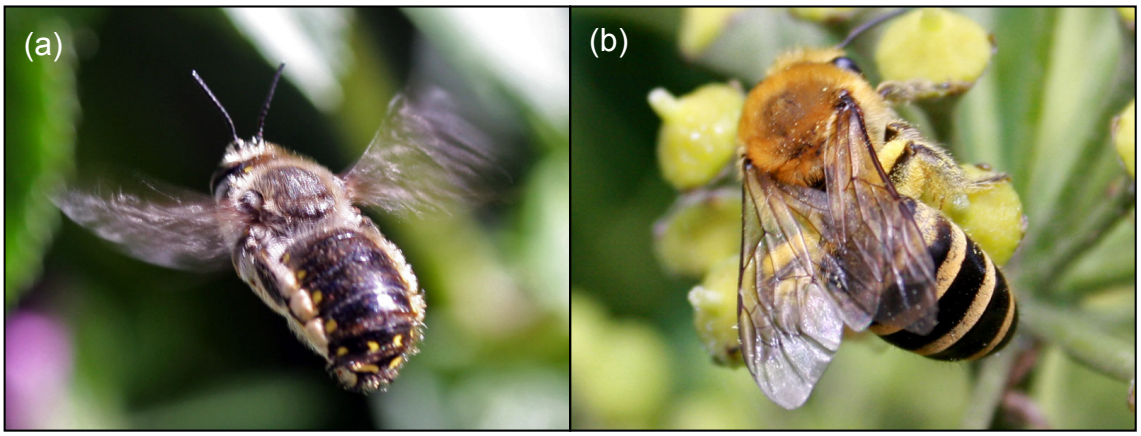


Figure 2.1. British solitary bees with characteristic appearance: (a) wool-carder bee, *Anthidium manicatum*, male hovering in patrol of his territory, (b) ivy bee, *Colletes hederae*, female foraging on ivy flowers.

Bumble bees have a characteristic 'stocky' body shape and from this can be easily identified to the *Bombus* genus. According to Edwards and Jenner (2009), there are 25 described *Bombus* species in Britain and most of them are impossible to identify definitively without capture. Indeed, two of the commonest species *B. terrestris* and *B. lucorum* are so similar to each other that even microscopic identification of pinned specimens with the use of a morphological key has a 5% misidentification rate of the former as the latter and 45% of the latter as the former (Wolf *et al.*, 2010). Fussell and Corbet (1992) developed a simple grouping system that allows categorization of British bumble bees into five broad groups based on the colour banding patterns, with each group represented by one or two main species that are common and several species that are rarer. The groups are: (a) two-banded white tails (main species *B. terrestris* and *B. lucorum*), (b) three-banded white tails (main species *B. hortorum*), (c) banded red tails (main species *B. pratorum*), (d) black-bodied red tails (main species *B. lapidarius*) and (e) browns (main species *B. pascuorum*) (Fig. 2.2a-e, Table 1 in Fussell & Corbet, 1992). This

allows the tentative assumption that most field observations can probably be attributed to the main species in each category. In addition, Britain was colonized by a new bumble bee species – the tree bumble bee, *B. hypnorum*, first spotted in Wiltshire, England, in 2001 (Goulson & Williams, 2001). It has since spread widely across much of England and Wales (BWARS, 2013) and has a unique banding pattern among the British bumble bees – brown thorax and black abdomen with a white tip, which makes it easy to identify to species unambiguously, even while actively foraging (Fig 2.2f).

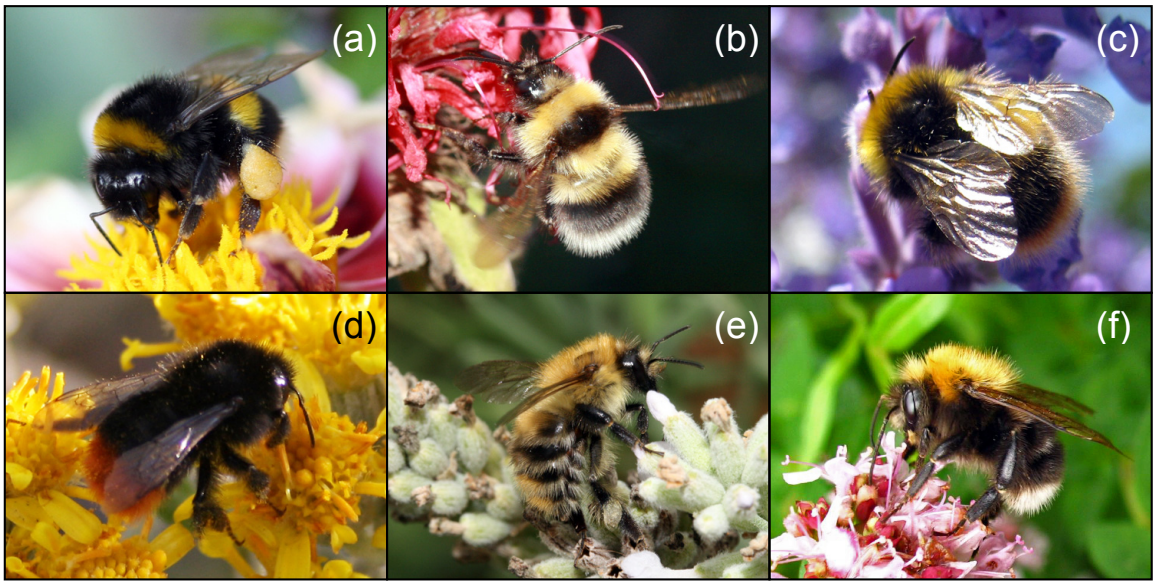


Figure 2.2. (a) *Bombus terrestris/lucorum* – a two-banded white tail. (b) *B. hortorum* – a three-banded white tail. (c) *B. pratorum* – a banded red tail (photo credit: Nicholas Balfour). (d) *B. lapidarius* – a black-bodied red tail. (e) *B. pascuorum* – a brown bumble bee. (f) *B. hypnorum* – the tree bumble bee that has a unique banding pattern among the British bumble bees (photo credit: Nigel Jones). Colour-band categories based on Fussell & Corbet (1992).

2.2.2. Hover flies and other true flies

After the bees, in many situations in Britain, the next commonest group of insects seen feeding on flowers are the true flies (order Diptera), and in particular, the hover flies (family Syrphidae). The British hover fly fauna comprises 271 described species and, as with bees, their reliable identification to species is often based on microscopic characteristics (Stubbs & Falk, 2002). Most hover flies are good mimics of stinging Hymenoptera: bees and social wasps (Fig 2.3). However, it is possible to distinguish them from their models and identify them to the Syrphidae family. The four key characteristics

distinguishing flies from bees and wasps are: (i) presence of only one pair of wings, (ii) absence of a narrow waist, petiole, (ii) considerably shorter antennae and (iv) bigger eyes, making up the bulk of a head in flies. In addition, foraging bees will often, though not always, be seen carrying pollen loads on their body, such as in the corbiculae of honey bees and bumble bees (e.g. Fig. 2.2a), or the underside of the abdomen in Megachilidae, which is never the case in flies.

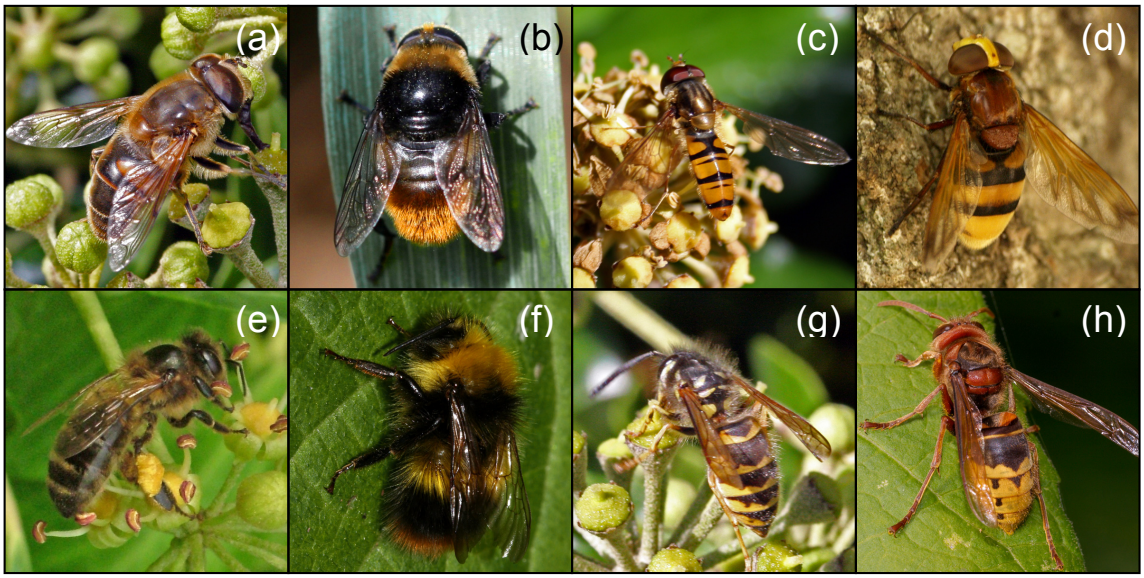


Figure 2.3. (a-d) Bee and wasp mimicking hover flies: (a) *Eristalis tenax*, (b) *Merodon equestris*, (c) *Episyrphus balteatus*, (d) *Volucella zonaria*, and (e-h) their respective models: (e) honey bee, *Apis mellifera*, (f) banded red-tailed bumble bee, *Bombus pratorum*, (g) social wasp, *Vespula vulgaris*, (h) European hornet, *Vespa crabro*. (Photo credits: (b, f) Sandy Rae, (d) Ferran Gort, (e) Francis Ratnieks, (h) Erik Jørgensen)

2.2.3. Butterflies and moths

Most butterflies and moths (Lepidoptera) feed on floral nectar as adults, while their larvae, caterpillars, are generally herbivorous. The wings of adult butterflies are covered in bright and often vividly colourful patterns (Fig. 2.4a-d), which makes their identification to species relatively easy. There are 60 butterfly species that occur in Britain, including both resident species and regular migrants (Thomas, 2014).

Moths are more diverse than butterflies, with about 2500 species known to occur in Britain, of which 874 are macro moths and c. 1600 are micro moths (Townsend *et al.*, 2007). The majority of moth species are nocturnal and, therefore, difficult to study.

Moreover, even at night time, the levels of moth activity on flowers can be very low. For example, Jacobs *et al.* (2010) quantified both diurnal and nocturnal insect visitation to ivy flowers and found that, while diurnal insects were abundant and active, only three individual moths were observed during the whole night of video recording: two of them spent little time foraging on flowers and one remained still for over 2 hours. However, some moth species are diurnal, or day-flying, and characteristic enough to be identified to species while visiting flowers (e.g. Fig 2.4e-h). Although there is no perfect definition of what constitutes a diurnal moth, 133 species of the British macro moths and are generally regarded as day-flyers (Newland *et al.*, 2013). Also, many micro moth species fly during the day, but these are often very difficult to identify or even see, as they are small and fly very quickly – it may be impossible to separate similar looking species even with the help of a good photograph (Newland *et al.*, 2013).

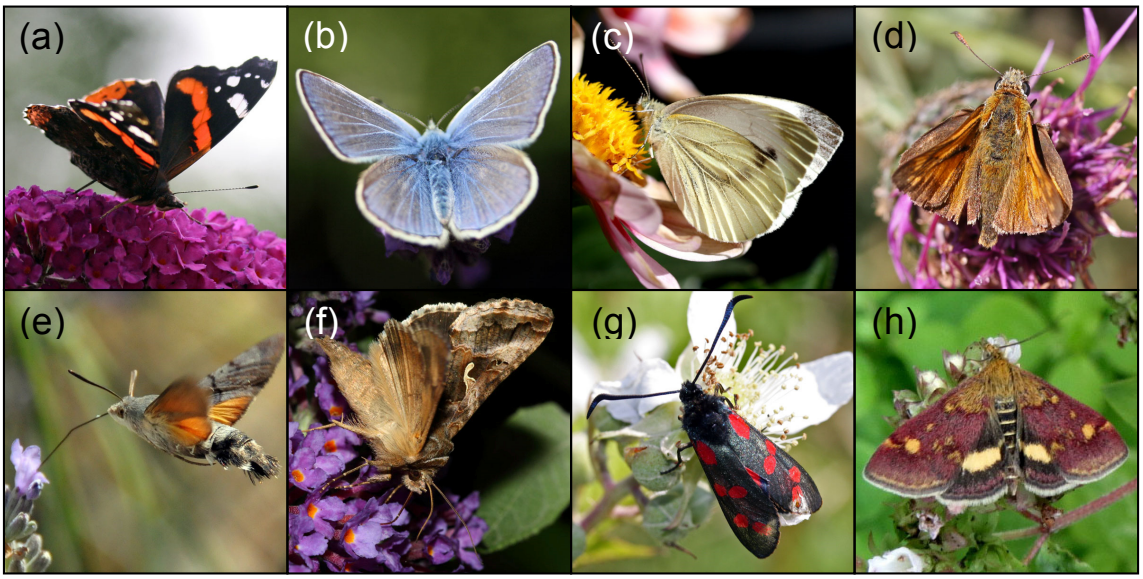


Figure 2.4. Common butterflies: (a) Red admiral, *Vanessa atalanta* (Nymphalidae), (b) Common blue, *Polyommatus icarus* (Lycaenidae), (c) Green-veined white, *Pieris napi* (Pieridae), (d) Large skipper, *Ochlodes sylvanus* (Hesperiidae), and diurnal moths: (e) hummingbird hawk-moth, *Macroglossum stellatarum*, (f) Silver Y moth, *Autographa gamma*, (g) Six-spot burnet moth, *Zygaena filipendulae*, (h) Mint moth, *Pyrausta aurata*. (Photo credits: (e) Frank Wouters, (f) Bob Hall, (h) David Short)

2.2.4. Other flower-visiting insects

Other insects, besides bees, flies, butterflies and moths are, in general, rarely seen feeding on floral resources. As part of the research carried out for this thesis, the insects observed

in this category typically comprised less than 1% of all flower-visitors and included both social, solitary and parasitic wasps, beetles and ants. A notable exception was the high abundance of social wasps on ivy flowers, which is discussed further in Chapter 8.

2.3. Studying honey bee foraging using observation hives

Hives that enable undisturbed observation of the internal workings of the honey bee colony have been described as early as seventeenth century (Showler, 1978). In 1920s, Rösch was among the first to have used observation hives to actually study honey bee behaviour (Rösch 1925 in Scheiner *et al.*, 2013). An observation hive is a variation of a regular movable-frame hive that houses one or more combs arranged vertically in a wooden frame behind a transparent screen, such as glass or, more recently, a thermoplastic (Scheiner *et al.*, 2013). There are many variations in the design of an observation hive, adapted for small to medium sized colonies and for use either indoors or outdoors (Showler, 1978). All observation hives in the Laboratory of Apiculture & Social Insects (LASI) used for research, including the research as part of this thesis, were made to custom specifications by Prof. Francis Ratnieks and contained four Langstroth frames: three medium and one deep (Fig. 2.5), which allowed for a colony size of up to about 5,000 bees. Conveniently, honey bees are sufficiently flexible behaviourally to accept this unnatural nest shape and will behave normally as long as a colony has a fertile queen to lay the eggs, workers have access to the outside and the hive is not exposed to low temperatures (Scheiner *et al.*, 2013).

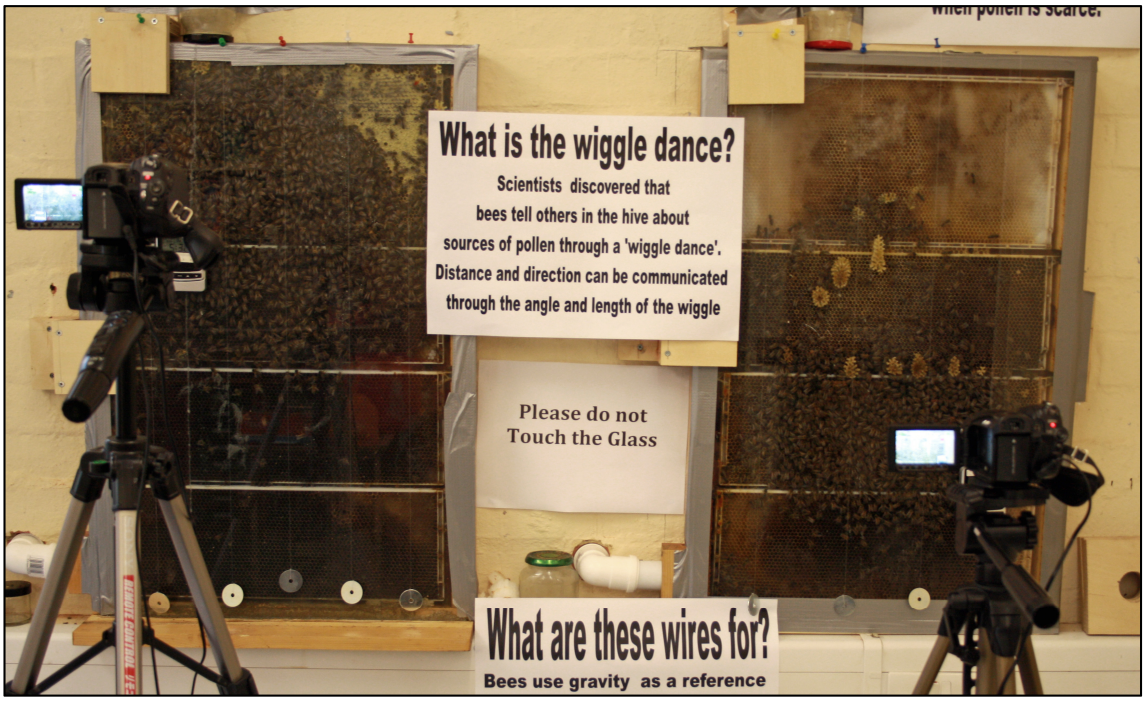


Figure 2.5. Two observation hives that were moved from the Laboratory of Apiculture & Social Insects (LASI) into the Dorothy Stringer School, Brighton, to study honey bee foraging in an urban environment. The hives had a dual benefit of both providing valuable research data and being a point of interest for school pupils.

2.3.1 The waggle dance

Honey bees perform many in-nest behaviours that can be studied with an observation hive. However, with regards to foraging, one particular behaviour that was used extensively in this thesis is their well-known waggle dance.

The waggle dance is a form of communication unique to honey bees (the whole genus *Apis*), whereby successful returning foragers communicate to their nestmates the location of a resource that a colony needs: nectar, pollen, water or resin (or a new nest site, in the case of swarms (Dyer, 2002)). The communicative role of the waggle dance was discovered by the Austrian ethologist Karl von Frisch, who spent most of his life studying this behaviour. His studies culminated in a landmark book "The Dance Language and Orientation of Bees" (von Frisch, 1967), and he was later awarded a Nobel Prize in Physiology in 1973 for his discovery. Although the "dance language", as von Frisch (1967) named it, is not strictly a language in a sense that it does not involve a set of symbols

governed by grammar, it has, nonetheless, been described as the most elaborate form of communication known in any animal, apart from humans.

The waggle dance involves a characteristic movement pattern consisting of two components: (i) a waggle phase, during which a bee rapidly shakes her abdomen sideways while taking a step forward, and (ii) a return phase, during which she walks in a loop to return approximately to the starting position (Fig. 2.6). Each waggle phase encodes the resource location from the hive or swarm in the form of a vector. The direction to the resource relative to the solar azimuth is given by the angle of the bee's body during the waggle phase relative to gravity. That is, a bee making a waggle run at 10° to the right of vertical is communicating resource located at 10° to the right of the solar azimuth. The distance is encoded in the duration of the waggle run, with a longer run indicating a greater distance, with each second corresponding to c. 750 m (Schürch *et al.*, 2013).

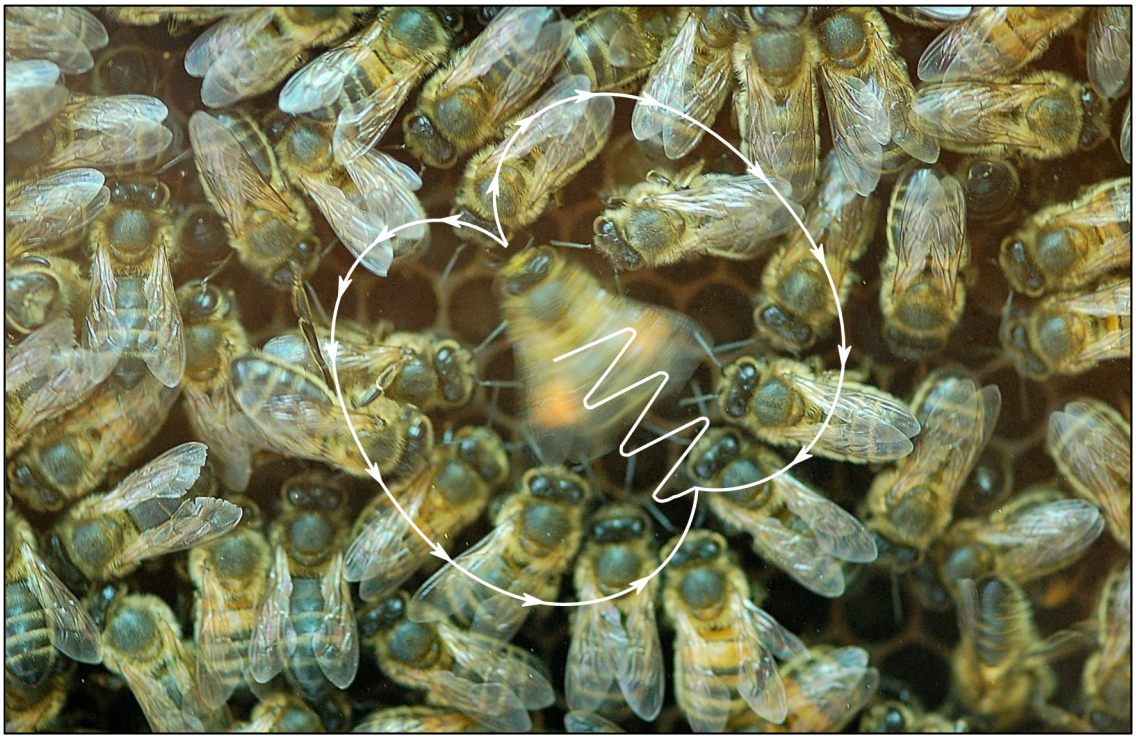


Figure 2.6. Honey bee forager performing a waggle dance on the vertical comb of an observation hive. At least seven nestmate bees in the photo above are following the dance to learn the encoded location communicated by the dancing bee. This particular dance indicates a resource located at c. 40° to the left of the current solar azimuth (Photo credit: Christoph Grüter).

Decoding waggle dances, therefore, presents an easy opportunity to 'eavesdrop' on honey bee foraging communications. But, one challenge for researchers decoding the dances in order to determine foraging locations is the presence of variation, or noise, in

both dance vector components. There are two sources of variation: (i) the intra-dance variation, with individual circuits being variable within a dance made by the same bee, and (ii) the inter-dance variation, with mean dance vector components being variable among dances made by different bees dancing for the same point location (e.g. an experimental feeder). The reason for the presence of this variation is interesting in itself and has been debated for a long time, with earlier work suggesting a 'tuned-error hypothesis', which states that dance imprecision is adaptive and serves to spread the recruits over a wider area, as opposed to a more precise area, which may be quickly depleted of resources (Towne & Gould, 1988). While more recent evidence suggests that the imprecision is a result of performance constraints, i.e. the bees are being as precise as they possibly can (reviewed in Couvillon, 2012; Preece & Beekman, 2014).

Over the years, developments in the methodology of decoding waggle dances have made it more efficient and accurate. Some of the earliest studies decoded waggle dances in real time, measuring the duration of a waggle phase with a stopwatch (e.g. Visscher & Seeley, 1982; Schneider & McNally, 1993; Steffan-Dewenter & Kuhn, 2003). Nowadays, we can easily record the dances using digital video cameras and analyse them on a computer (Fig. 2.7). Modern video cameras are capable of recording video at a rate of at least 24 frames per second, thus allowing for a temporal resolution as high as 1/24th of a second or greater. A dancing bee may repeat a complete circuit for a maximum of 100

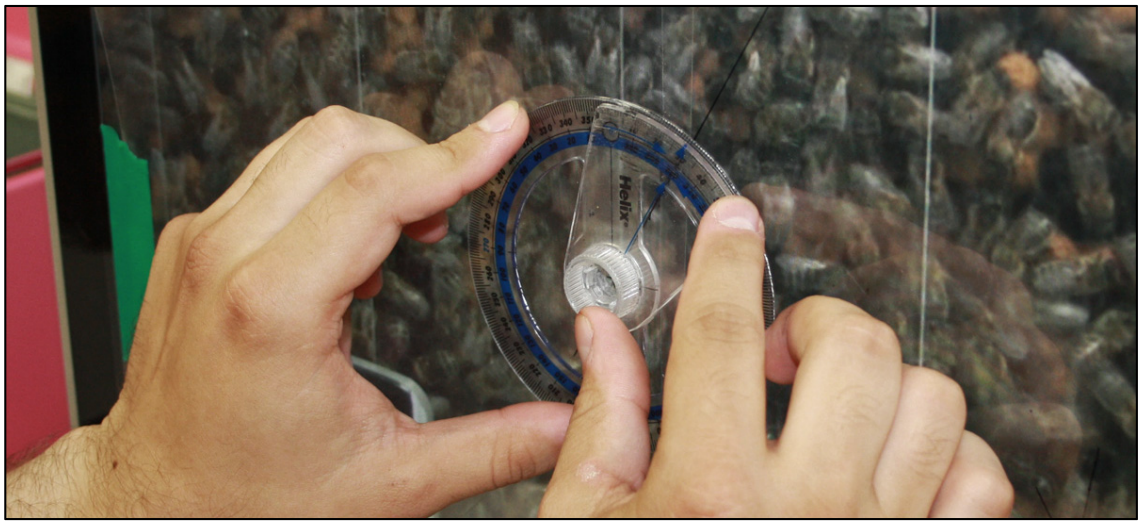


Figure 2.7. Waggle dances being decoded by framewise video playback on a computer. The waggle phase orientation is measured using a protractor, and its duration is measured using a software timestamp.

times or more. However, there is no need to decode every circuit within a dance to get an accurate average. Couvillon *et al.* (2012) showed that waggle runs of four consecutive circuits offer a good approximation of the whole dance, provided the first and the last circuits are not included, as they are significantly more variable than the middle circuits. Both the mean duration and the mean angle of these four runs correlate exceptionally tightly with the corresponding parameters of the whole dance (Pearson's r = 0.986 for duration and 0.998 for angle, Couvillon *et al.*, 2012), and thus present a very accurate proxy.

In addition, Schürch *et al.* (2013) have developed a method of taking into account the imprecision inherent in waggle dances when studying the overall foraging patterns of a colony. Given the variability in both dance vector components, the point location indicated by each dance can be simulated a very large number of times using the Markov Chain Monte Carlo algorithm. These simulated locations plotted on a map can be binned into grid sectors to yield a spatial probability distribution, or a 'heat map'. For example, Figure 2.8 shows a joint probability distribution of several dances advertising the location of an experimental feeder, which provides an accurate representation of the actual location encoded in these dances and the variation associated with it. Additionally, this

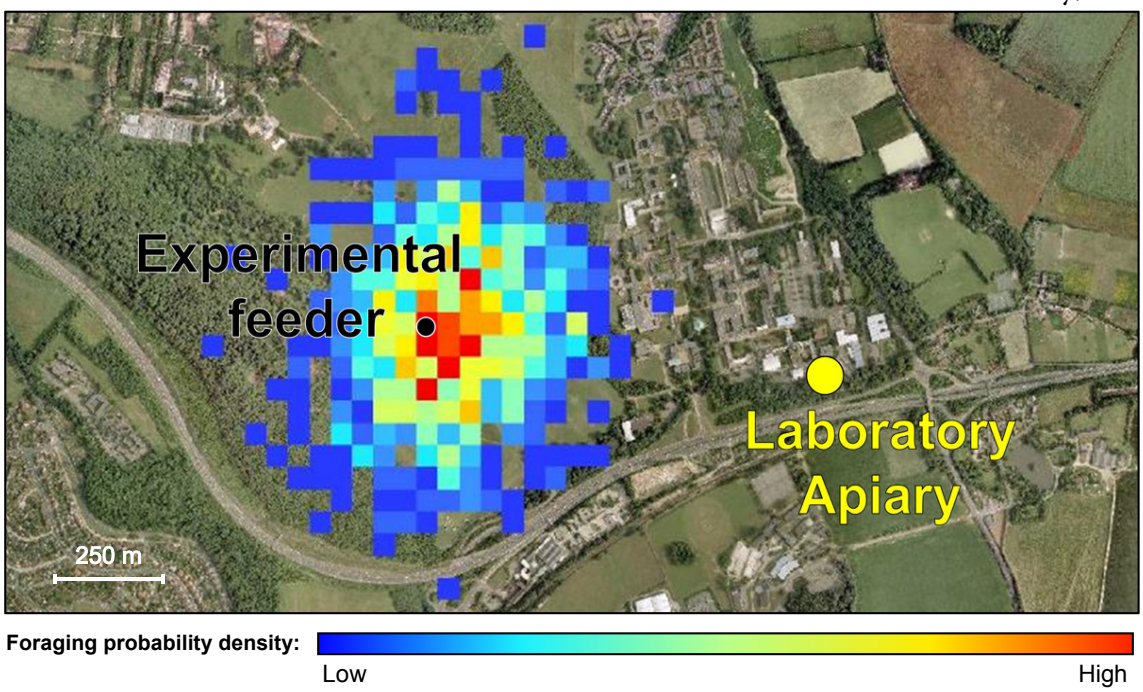


Figure 2.8. Joint probability distribution, binned into 25 x 25 m grid sectors (on an arbitrary scale from low probability (blue) to high (red)), of several waggle dances advertising the location of an experimental feeder c. 500 m from the study hive located in the laboratory apiary (adapted from Schürch et al. 2013).

methodology allows estimation of a proportion, with a confidence interval, of dances pointing to areas of interest, such as urban areas (Chapter 10) or fields of oilseed rape (Chapter 11).

It was briefly mentioned above that waggle dances indicate locations of resources sought by a colony. But which resources are they and how should the dance data be interpreted? By far, the biggest resource that a colony needs is food: nectar and pollen. The two other resources collected by foragers are water, used for evaporative cooling on hot days, and resin, used for reinforcement, insulation and sanitation of the nest. Seeley (1995) reported that, although estimates vary, an average colony extracts from its environment each year about 120 kg of nectar, 20 kg of pollen, 25 litres of water and only about 100 g of resin. However, not every successful forager makes a waggle dance. For example, with regards to foraging for nectar, which has been studied most extensively, the probability of dancing is directly proportional to the value of the source. Dances for highly valuable sources are also repeated for a greater number of circuits, leading to greater recruitment of nestmates to these sources and a higher probability of detecting these dances in a sample. This decision-making process is based on both the forager's private information, which includes factors such as the sweetness of nectar, flower handling time in a patch and its distance to the hive, and the social information, which takes a form of the delay between arriving to the hive and meeting a one of the receiver bees who help to unload the nectar (reviewed in Seeley, 1995; Dyer, 2002). High delay times indicate either that there is a high flow of nectar from the environment, or that the colony is already full of nectar, both of which tend to diminish the relative value of a source, as being assessed by a forager. Thus, a sample of waggle dances represents not all foraging locations used by a colony, but only the most valuable foraging locations, where a value is judged based on (i) the intrinsic profitability of a resource, (ii) the profitability of other resources discovered in the environment by nestmate foragers and (iii) the current needs of the colony (Dyer, 2002).

2.4. Studying honey bee foraging using pollen collection and identification

Another way to study honey bee foraging is to analyse pollen collected by foragers. Complementing the information encoded in waggle dances, pollen analysis can be used to determine the relative abundance and identity of the plant species on which the bees have been foraging. However, although foragers often collect both nectar and pollen on the same foraging trip, some collect either nectar or pollen only (Ribbands, 1953). Indeed, some plants, such as poppies (*Papaver* spp.), peonies (*Paeonia* spp.) or the kiwi-fruit (*Actinidia deliciosa*), naturally produce no nectar and can only be used as pollen sources (Proctor *et al.*, 1996). Other plants produce tiny amounts of pollen (e.g. *Lavandula*, pers. obs.) and thus are mainly used as nectar sources. Furthermore, honey bees clearly have preferences for some types of pollen over the others. For example, Schmidt (1982) showed using greenhouse preference trials that the pollen of almond (*Prunus dulcis*) and maple (*Acer grandidentatum*) is preferred over pollens of several other plant species, including creosote (*Larrea tridentate*), dandelion (*Taraxacum* sp.) and pine (*Pinus halepensis*). But, the underlying reasons for these preferences are not clear (Schmidt, 1982). Since pollen is normally the sole source of protein for the colony, one hypothesis states that the preferences are influenced by its protein content. However, Pernal and Currie (2001, 2002) suggest that individual foragers are unable to assess the protein content of pollen. Using a large dataset of 377 plant species from 93 families, Roulston *et al.* (2000) showed that the protein content of pollen ranges considerably, between 2.5% and 61%, and, although, it is, on average, higher in animal-pollinated species (39%) than in wind-pollinated species (26%), there is no statistically significant difference when phylogeny is taken into account. In other words, the plants do not appear to have responded evolutionarily to animal pollination by increasing the reward value of their pollens. Instead, the pollen protein content appears to be mainly governed by the need to grow a pollen tube through a style (Roulston *et al.*, 2000).

As mentioned above, a honey bee colony over the course of a year needs much less pollen than nectar. The rate of pollen collection is related to the amount of brood being reared and can vary substantially. For example, in one sample of six hives, the proportion of foragers that collected pollen ranged from 28 to 95%, with a mean of 69% (Filmer, 1932 in Ribbands, 1953). However, the amount of pollen stored in the comb is maintained around a homeostatic set-point, which is c. 1 kg in a typical strong colony (Fewell & Winston, 1992). At this amount, pollen foraging is greatly reduced and nectar foragers that get dusted in pollen while visiting flowers may even discard it entirely by brushing it off their bodies (Thorp, 2000). In conclusion, given that pollen foraging differs from nectar foraging in several important respects, a sample of pollen collected by the colony is best viewed not as a comprehensive sample of all floral foraging sources, but rather as a supplement to other types of data, such as the waggle dance data.

2.4.1 Pollen collection and identification

A sample of pollen collected by a honey bee colony can easily be obtained through pollen trapping (Dimou *et al.*, 2006). A pollen trap is a mesh with square or circular holes, c. 5 mm in diameter, which is placed in front of the entrance to a hive (Fig. 2.9). The holes are

Figure 2.9. Pollen trap placed onto the entrance tube of an observation hive at the Laboratory of Apiculture & Social Insects. Pollen loads are knocked off the corbiculae of returning foragers as they pass through the mesh and are collected as they drop into the tray below.

just wide enough for returning foragers to pass through, while pollen loads get knocked off their corbiculae, or pollen baskets, and drop down into the collection tray below.

Conveniently, the proportions of pollen collected from various plant species can be estimated at the level of pellets, rather than the level of individual pollen grains. This is because the overwhelming majority of pellets (95% to 99%) are typically monofloral, containing pollen of only one plant species (Seeley, 1985 and references therein). This is almost certainly due to the fact that honey bee foragers exhibit a high degree of flower constancy (reviewed in Chittka *et al.*, 1999). That is, individual foragers tend to visit flowers of the same species with high fidelity, even if flowers of other species occur in the same patch. Furthermore, honey bees show an even greater fidelity when collecting pollen than when they are collecting nectar, because of the extra difficulty in packing pollen from more than once source into the same pellet (Zahavi *et al.*, 1984 in Proctor *et al.*, 1996). However, some caution needs to be exercised, as this method assumes that pellets originating from different plants do not, on average, differ in size. While this assumption is generally true, with dry pellet weight at c. 5-6 mg, there are exceptions: e.g. pollen of upland cotton, *Gossypium hirsutum*, is relatively difficult for honey bees to pack and results in significantly lighter pellets, c. 0.4 mg (Vaissière & Vinson, 1994).

Pollen pellets are also variable in colour (Fig. 2.10). Hence, one way to identify their plant sources is to use a colour key, such as that developed by Kirk (2006). However,

Figure 2.10. A sample of pollen pellets brought to the colony by honey bee foragers, collected using a pollen trap positioned at the hive entrance.

identification based on colour is a rather crude and inaccurate method, as the colour is not only slightly variable within a species, but also overlaps among species (e.g. many plant species have yellow pollen) and is affected by the pellet water content (pollen is moistened with nectar as it is packed into a pellet), which, in turn, is affected by microclimate and, also, the light conditions under which a pellet is viewed (Kirk, 2006).

A more reliable way to identify the pollen plant sources is to examine the morphology of the pollen grains microscopically. Pollen morphology varies considerably among species in traits such as size, shape and the structure of the exine (the outer layer), including the sculpturing of the surface and the number, position and the type of apertures: pori (pores) and colpi (furrows) (Moore *et al.*, 1991). There exist morphological keys for pollen identification. However, the key of Moore *et al.* (1991), for example, covers only some of the more important and common taxa found in North America, northwestern Europe and some of the Mediterranean areas, which is far from a complete coverage of these regions. Indeed, Moore *et al.* (1991) themselves suggest that the research where accuracy of identification is important should never rely on keys and photographs alone, but should always confirm the identity by comparison with the type specimen.

Studies exploring bee-collected pollen floras rely heavily on extensive pollen reference collections specific to their study area (e.g. Ireland: Coffey & Breen, 1997; Argentina: Andrada & Tellería, 2005; Greece: Dimou & Thrasyvoulou, 2007; Italy: Aronne *et al.*, 2012; Oman: Sajwani *et al.*, 2014). But even the use of a reference collection may have shortcomings. The pollen morphology within some plant groups is so similar that it may only be possible to identify pollen to a high taxonomic rank, such as genus or family (particularly in difficult groups – Rosaceae and Asteraceae). In some cases, pollen can remain completely unidentified (e.g. Baum *et al.*, 2011).

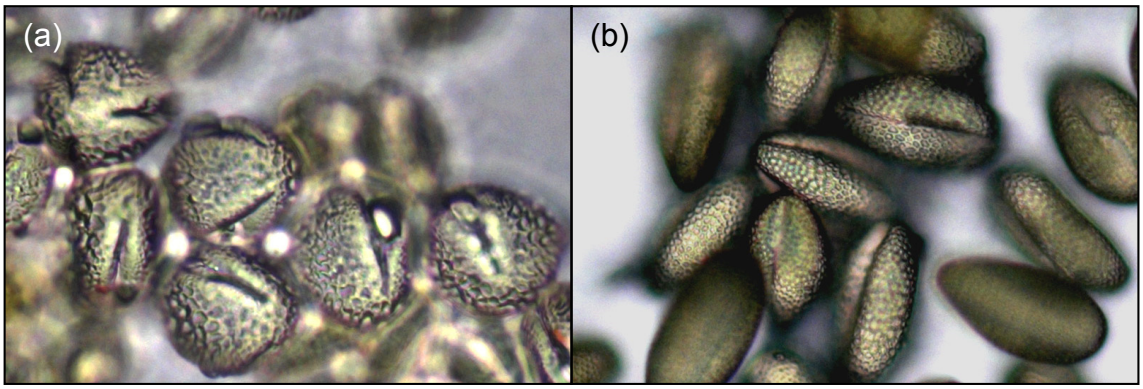
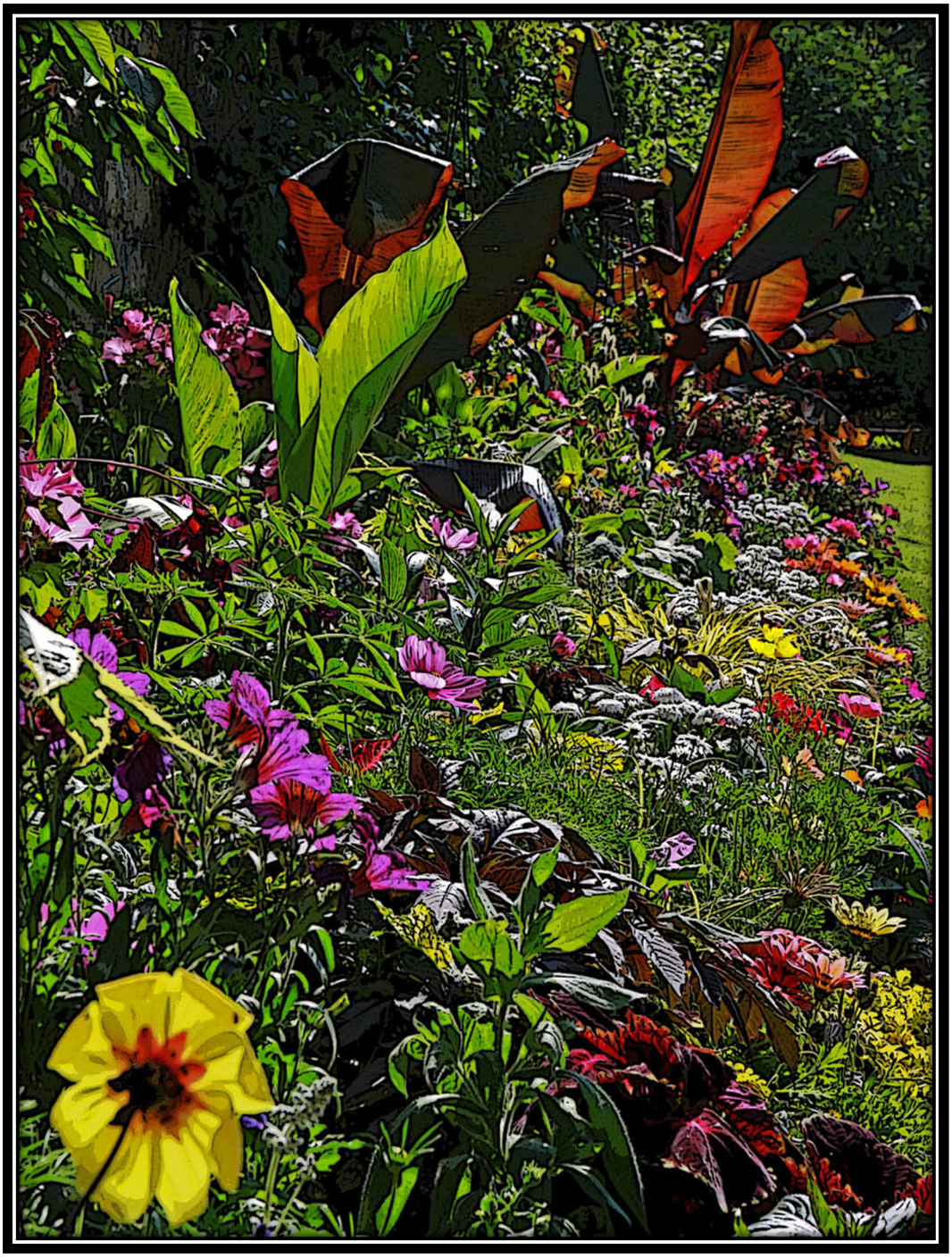


Figure 2.11. Pollen grains of (a) ivy, *Hedera* sp., and (b) oilseed rape, *Brassica napus*, under bright-field light microscopy at ×400.

In the absence of a local reference collection, and due to the study questions being focused on the particular species, Chapters 8 and 11 identified only ivy (*Hedera* spp., Fig. 2.11a) and oilseed rape pollen (*Brassica napus*, Fig. 2.11b), respectively, by reference to the type specimens collected locally.

Research Chapters

Part 2: Garden Plants and their Attractiveness to Flower-Visiting Insects



Chapter 3

Listmania: the strengths and weaknesses of lists of garden plants to help pollinators

Mihail Garbuzov, Francis L. W. Ratnieks

Abstract

Pollinators are in global decline. One of the few ways in which the general public can help is by cultivating ornamental garden plants that attract pollinators by producing nectar, pollen, or both. Advice in the form of lists of recommended plants is available, but how good are these recommendations? Here, we overview a sample of 15 such lists and discuss their strengths and weaknesses. In particular, we found that the range of the number of plant genera per list was large (29–257) and that there was rather little overlap in the recommendations, even among lists addressing the same geographic region (e.g. Britain or North America). Furthermore, the lists often included poor recommendations, omitted many good plants, lacked detail, and were almost invariably based on their authors' general expertize rather than on empirical data. Nevertheless, some advice given in the lists was good, because these recommendations were presumably backed by personal observations and less formally gathered data. The lists were also very appealing to the public, which makes them an excellent tool in communication and a useful starting point for further research.

Introduction

Many pollinators are in global decline. The causes are mostly associated with human activities, such as land-use intensification and the spread of alien species and diseases (Potts *et al.*, 2010a; Winfree *et al.*, 2011; Vanbergen & the Insect Pollinators Initiative,

2013). One of the few ways in which the public can help is by growing bee- and pollinator-friendly plants in their gardens. Although urbanization is generally disadvantageous for wildlife (McKinney 2008), especially compared with pristine natural habitats, it has been shown that urban green spaces often harbour considerable biodiversity (Angold *et al.*, 2006). Among all types of urban green space, domestic gardens are probably the largest and most important component (Davies *et al.*, 2009; Goddard *et al.*, 2010; Owen, 2010).

In the United Kingdom, gardening is a popular hobby, and the public interest in helping pollinators is mirrored, for example, in an initiative of the Royal Horticultural Society launched in 2011 that lists selected ornamental plants and labels them with the Perfect for Pollinators logo [www.rhs.org]. Numerous other lists and recommendations are available through leaflets, pamphlets, information stands, books, Web sites, and even television programs (Fig. 3.1). But how good are these recommendations? A list is only as good as the data that went into it. However, to our surprise, such lists almost never refer to the empirical sources on which they are based and may have other shortcomings. For example, Thompson (2006) described one list compiled by Natural England, a government-funded agency responsible for the protection and improvement of the

Figure 3.1. Promotion of pollinator friendly plants. (a) The selection of *Bee Friendly* plants on sale in a UK garden centre. The photograph of a "bee" on the yellow sign in the centre is actually a hover fly. (b) *Sedum* 'Rose Carpet,' which is attractive to bees, sold in pots bearing the (c) *Bee Friendly* logo. (d) Plant labels bearing the Royal Horticulture Society *Perfect for Pollinators* logo. (e) Information leaflets with advice on helping bees and butterflies in British gardens featuring a photograph of a monarch butterfly that does not occur in Britain. (f) Information stand on helping to save bees, including a quote attributed to Albert Einstein, stating that the "human race would have no more than four years to live if bees disappeared," which it seems he never said (Calaprice, 2010). Photo credits: Francis Ratnieks.

natural environment, as looking "very much as if it was put together late one Friday afternoon" (p. 54). Here, we evaluate a selection of 15 lists of plants recommended to attract flower-visiting insects to gardens and discuss their strengths and weaknesses.

A sample of lists

In making our sample of lists of recommended garden plants, we simulated an enthusiastic gardener searching the Internet on Google and the Amazon online bookstore using the following English keywords and combinations: *bee*, *butterfly*, *pollinator*, *garden*, *plant*, *flower*. The lists that we found were written by both lay or amateur authors and professional or semi-professional organizations (Fig. 3.2). We included all of the latter category and most of the former. In particular, we omitted unpublished lists that were available only on web sites, which were often without a clear author. Most of the lists that we found were aimed at Britain and the others at the United States or Canada.

When we compared and overviewed the lists, we found that it was most practical to do so at the plant genus level. In part, this is because many of the recommendations were given at this level, perhaps implying that all or most species in the genus are equally or almost equally good (e.g. *Aster*, *Lavandula*). In addition, some of the recommended

Figure 3.2. Some of the lists of bee-, butterfly-, and insect-friendly plants analysed in this chapter. The top row shows lists produced by organizations with standing in plants or pollinators: from left to right, UK's Royal Horticultural Society (RHS 2011), Natural England (2007), the Xerces Society (2011). The bottom row shows lists produced by individuals and published as books: from left to right, Lavelle and Lavelle (2007), Hooper and Taylor (2006), Baines (2000).

plants are hybrid varieties of horticultural origin, for which the distinction between species is unclear. Many such varieties, once bred, are propagated vegetatively, and it is not uncommon for the information on their parentage to have become lost and unknown even to experts. Indeed, parentage can be a well-guarded commercial secret in newly developed varieties.

The 15 lists included in our sample are shown in Table 3.1. The number of recommended genera per list ranged from 29 to 257, with 455 in total across all of the lists. Eight lists were compiled by lay authors and seven by organizations with standing or authority in plants or pollinators. Ten were for Britain and five for North America.

Table 3.1. Sample of 15 lists selected for overview

Reference	Number of genera	Type of insect	Geographic region	Author credentials
Thurman (1994)	69	Pollinating insects*	Britain	Lay
Gibbons and Gibbons (1996)	69	Pollinating insects*	Britain	Lay
Baines (2000)	127	Pollinating insects*	Britain	Lay
Hooper and Taylor (2006)	140	Bees	Britain	Lay
Ellis (1997)	116	Butterfly adults	North America	Lay
Merilees (2000)	29	Pollinating insects*	North America	Lay
Creeser (2004)	92	Pollinating insects*	North America	Lay
Lavelle and Lavelle (2007)	162	Pollinating insects*	North America	Lay
Vickery (1998)	87	Butterfly adults	Britain	Professional
Xerces Society (2001)	88	Pollinating insects	North America	Professional
Natural England (2007)	130	Pollinating insects*	Britain	Government
Countryside Council for Wales (CCW 2008)	116	Pollinating insects*	Britain	Government
International Bee Research Association (IBRA 2008)	257	Bees	Britain & Western Europe	Professional
Royal Horticultural Society (RHS 2011)	198	Pollinating insects	Britain	Professional
Bumblebee Conservation Trust (n.d.)	68	Bumble bees	Britain	Professional

*In cases where the scope of the list included other wildlife (e.g. birds), only plant genera explicitly recommended for pollinators were included

The weaknesses of the lists

Overlap among the lists was not high

The overlap in the recommended genera among the lists was not very high. Over half of the total genera recommended across all of the lists (233 of 455, 51%) were present in only one or two lists, and over a third (165 of 455, 36%) were in just one list (Fig 3.3). No single genus was present on all 15 lists, whereas only a few were present on 10 or more lists (38 of 455, 8%).

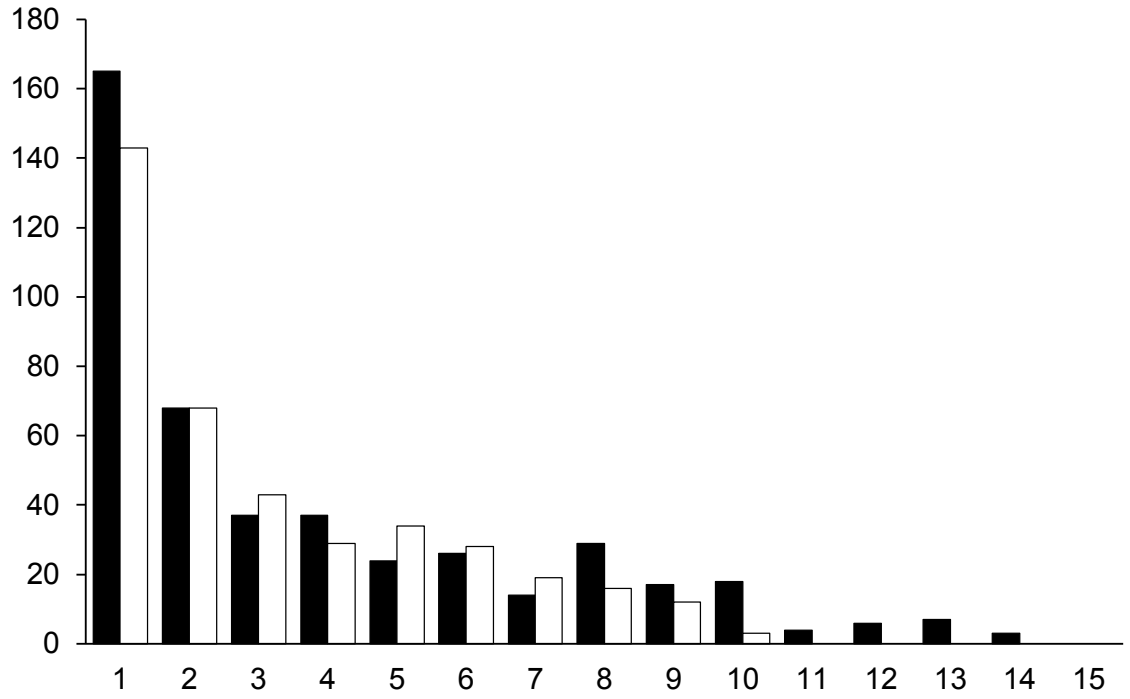


Figure 3.3. Overlap in plant genera recommended as attractive to pollinating insects in the 15 garden plant lists from Britain and North America combined (the black bars) and the 10 British lists alone (the white bars). The bars show the number of genera included in exactly that number of lists.

This pattern is unlikely to be because of combining lists from two distinct geographic areas, because a similar pattern was also seen in the 10 British lists. Only 3 of 395 genera—less than 1%—were present in all of the lists, whereas over half (211 of 395, 53%) were present in one or two lists, and over a third (143 of 395, 36%) was in just one list (Fig. 3.3).

One obvious reason why the overlap among the lists was not higher is that the authors did not agree on which plants are attractive. There were also other possible explanatory factors. For example, some of the lack of overlap may have been due to the geographic region. North America is much larger and more climatically diverse than Britain. It is probably not easy to recommend plants that would do well across the whole range of climates, and this may be the reason for which we found fewer North American lists. For example, milkweed (*Asclepias* spp.) was often found in the North American lists, but not in any of the British lists, because it is poorly suited to the local conditions; does not survive the winter; has a high chance of not flowering at all in a season; and, as a consequence, is rarely grown. Nevertheless, there was considerable overlap between the

regions: almost half (202 of 455, 44%) of all of the listed genera were found in at least one list from each region.

In addition, some of the lack of overlap among the lists may have been due to their scope, as some were focused on adult butterflies or bees, whereas others were for insect pollinators in general. However, even the lists with different scopes were in some agreement, probably because different types of insects, such as butterflies and bees, often visit the same plants for nectar.

Furthermore, some of the non-overlap may have been due to the changes in plant taxonomy, such that the same plant species were reclassified into other genera and were recommended under different binomial names by lists before and after the reclassification event. For example, many species that were formerly in the genus *Aster* have been reclassified into the genus *Symphyotrichum* (Harms, 2002). However, to our knowledge, such events were infrequent relative to the large number of recommendations in the lists and were unbiased with respect to the plant's attractiveness to pollinators. Therefore, it is probably a very minor factor in the overall picture.

The lists lacked detail on how they were compiled

With one exception, the lists that we overviewed did not include any information, by way of reference or otherwise, on how the authors determined the plants' attractiveness to pollinators. The exception was the list of 100 best plants for butterflies by Vickery (1998), which referred to a research survey carried out by Butterfly Conservation. However, to our knowledge, the analyses of the results of this survey have not been published in peer-reviewed literature, although the results were briefly summarized in a chapter of an edited volume (Vickery, 1995), whereas the exact same list remains current on the Butterfly Conservation web site more than 15 years later. In all other lists, the authors have left the reader to assume or conclude that the plant recommendations were based on their

personal opinion, derived presumably from a number of sources, including personal experience, reading, and quite likely through the influence of other lists.

Furthermore, the lists seldom provided any information on the relative attractiveness of the plants that they recommended. A reader might, therefore, assume that all plants recommended are equally or almost equally attractive to pollinators, although this is almost certainly not the case. Again, the only exception was Vickery (1998), which ranked the plants in descending order of attractiveness. Our own research has shown that garden plants, even those that are often recommended in lists, can vary greatly in the number of flower-visiting insects that they attract (Chapter 5: Garbuzov & Ratnieks, 2014a).

Poor plants were sometimes recommended

Some plants included in the lists were not particularly good for other reasons. For example, teasels (genus *Dipsacus*), although they attract some flower-visiting insects, are biennials that do not produce flowers in the first year of their life cycle and that have a relatively short flowering period in the second year (Fig. 3.4a). Petunias (*Petunia* × *hybrida*), included in the list of Lavelle and Lavelle (2007), have particular cultivars that have been empirically shown to attract relatively few pollinators, despite having large standing crops of nectar (Corbet *et al.*, 2001).

Thompson (2006) noted that some lists rely heavily on nativeness as a criterion of friendliness for wildlife. As a result, this includes plants that are unattractive from the human perspective and that are therefore unsuitable as ornamental garden plants. Indeed, some of the recommended plants, such as clovers (*Trifolium* ssp.; Fig. 3.4b) and dandelions (*Taraxacum* ssp.), are regarded as weeds by many gardeners. In addition, many of these native plants are rare and difficult to obtain, even from specialist suppliers, and so are effectively unavailable to the typical gardener (Thompson 2006).

Figure 3.4. Recommended ornamental garden plants illustrating specific points. (a) Teasel, *Dipsacus fullonum*, a native British insect-attractive plant, which is biennial and so flowers only in the second year of its life cycle and dies. (b) White clover, *Trifolium repens*, a native British plant attractive to bees, which is not suitable for planting in flowerbeds, but can be allowed to grow in lawns. (c) *Dahlia* 'Bishop of Llandaff,' a plant from Mexico that is considerably modified by breeding and was seldom recommended in the surveyed lists but that is very attractive to bumble bees and other pollinators. (d) Yellow loosestrife, *Lysimachia vulgaris*, which was rarely recommended, visited by *Macropis europaea*, a solitary bee that specializes on this plant. (e) Marjoram, *Origanum vulgare*, a species native to Britain that is very attractive to insects and was recommended in almost all (14 of 15) of the lists. (f) Lavender (*Lavandula*), a Mediterranean plant that is very attractive to British bees and that was recommended in most (13 of 15) of the lists in our sample. Photo credits: (d) Albert Krebs, (a-c, e,f) Francis Ratnieks.

There has been a long-standing belief that only native plants are useful to native wildlife (Comba *et al.*, 1999a). Although this may be true in certain parts of the world, such as Australia, Madagascar, or Hawaii, where the majority of plant and animal species are endemic, it is generally not the case in the temperate regions, including Britain (Thompson 2006). For example, the survey carried out as part of the BUGS (Biodiversity in Urban Gardens in Sheffield) project in the United Kingdom showed that a substantial proportion—on average 55%—of the plant species found in domestic gardens are non-native (Smith *et al.*, 2006a). However, neither the species richness nor the abundance of invertebrates generally correlates with either native or alien plant richness (Smith *et al.*, 2006c; Smith *et al.*, 2006b). Because the main reward component of nectar is sugar (Nicolson & Thornburg, 2007), many nectarivores will visit non-native flowers as readily as the native ones. For example, the bumble bee *Bombus terrestris*, introduced to Australia, is thriving in local ecosystems and is known to visit flowers of at least 66 native plant species from 21 families (Kingston & McQuillan, 1998). Similarly, the European

honey bee, *Apis mellifera*, may forage on over 100 plant species, both native and exotic, in any one geographic region (Goulson, 2003 and references therein), whereas Crane (1990) estimated the total number of flowering plant species used by the honey bee at around 40,000 worldwide. In the urban gardens of the New York City, Matteson and Langellotto (2011) showed that small-scale experimental additions of native plants failed to increase bee and butterfly species richness, while pollinators heavily used introduced ornamental and crop plants for floral resources. In addition, our own recent research showed that exotic ornamental garden flowers can be as attractive as—or even more attractive than—native flowers to native flower-visiting insects (Fig. 3.4c,f; Chapter 5: Garbuzov & Ratnieks, 2014a).

Although the breeding of ornamental varieties can reduce their value to insect flower visitors, such as by the doubling of petals, which reduces the amount and accessibility of floral rewards (Comba *et al.*, 1999b; Corbet *et al.*, 2001; Garbuzov & Ratnieks, 2014a), it is not always the case. For example, the hybrid varieties of lavender (*Lavandula* × *intermedia*) attract more insects than their non-hybrid counterparts (*Lavandula angustifolia*) (Chapter 5: Garbuzov & Ratnieks, 2014a). In other cases, hybrid sterility may cause the inability to set seed and may therefore result in a longer flowering period—in some cases, resulting in almost continual flowering (e.g. *Erysimum linifolium* 'Bowles' Mauve') (Chapter 5: Garbuzov & Ratnieks, 2014a).

Many good plants were omitted

Many plants attractive to pollinators were often not included in the lists. For example, open-flowered varieties of *Dahlia*, as well as *Agastache* and *Borago* were among the most attractive plants to insects in a recent quantitative study (Chapter 5: Garbuzov & Ratnieks, 2014a), but were not included in over half of the lists in our sample. However, with many thousands of plant varieties available to gardeners (Cubey & Merrick, 2011), many of which are attractive to pollinators, it is likely that no list can ever be complete. We

therefore agree with an important point previously made by both Thompson (2006) and Gaston *et al.* (2007) that lists can implicitly convey the wrong impression—namely, that the plants not included are of little value to pollinators. This is certainly not the case.

Although many pollinators are generalists with respect to the type of plant that they will visit, some are specialists dependent on one or a few plant species or related genera (Johnson & Steiner, 2000). These plants may not necessarily attract a wide range of insects and, as a result, will not usually be included in a typical list, but they can have a place in gardens, especially if the plants are attractive in their own right and offer an opportunity to observe and aid insects that are of special interest or are rare. For example, Baldock (2008) reported that mignonette (*Reseda lutea* or *Reseda luteola*) in a garden attracted oligolectic *Hylaeus signatus* (Müller *et al.*, 2006), although this bee species was not previously recorded in the area. Plants in the genus *Lysimachia*, such as the yellow loosestrife (*Lysimachia vulgaris*), are reputed to be a magnet for highly specialized *Macropis* bees (Fig. 3.4d), of which the females provision their offspring with loads of pollen and floral oils, collected from special structures (trichome elaiophores) instead of with nectar (Simpson & Neff, 1983; Celary, 2004).

The strengths of the lists

Many recommendations were good

Many of the recommendations included in the lists were good. This is particularly true for the plant genera that were present in several of the lists—that is, the genera included in a large proportion—two-thirds or more of the lists in our sample—such as *Origanum* (Fig. 3.4e), *Sedum*, and *Solidago* (Table 3.2). This shows that even recommendations based on personal opinion can be valuable, because they will likely be based on years of general observation and experience. The top 38 most frequently recommended genera constituted only 8% of the total 455 genera recorded in the list sample. However, half of

these featured in at least one research study that empirically showed their attractiveness to pollinators (Table 3.2). Although most recommendations in the lists were not based on hard data, they can provide a useful starting point for future research. Future lists could be improved by greater reliance on empirical studies (e.g. such as those cited in Table 3.2). Future studies might also use citizen science data collection, because the necessary protocols are quite simple.

Table 3.2. Thirty-eight most frequently recommended genera, included in 10 or more lists, out of the total 455 genera in a sample of 15 lists. Four rightmost columns indicate availability of empirical data showing high attractiveness to pollinators of at least one member of the plant genus.

Plant genus	Number of lists recommended	S.A. Corbet group papers[a]	G.W. Frankie group papers[b]	D. Tommasi paper[c]	M. Garbuzov & F.L.W. Ratnieks papers[d]
Origanum	14	x	x	x	x
Sedum	14				
Solidago	14		x		
Aster	13		x		
Ceanothus	13		x		
Centaurea	13	x	x	x	
Dianthus	13				
Erysimum	13				x
Lavandula	13		x		x
Mentha	13				
Amelanchier	12				
Lonicera	12				
Malus	12		x		
Prunus	12		x	x	
Scabiosa	12	x	x		
Thymus	12				
Buddleja	11				
Echinops	11				
Salix	11				
Viburnum	11				
Achillea	10		x		x
Allium	10				
Aubrieta	10				
Cotoneaster	10			x	
Crataegus	10				
Dipsacus	10	x			
Eschscholtzia	10		x		
Eupatorium	10	x			
Geranium	10				
Hedera	10		x		x
Helianthus	10		x		
Heliotropium	10				
Iberis	10				
Limnanthes	10				
Lobularia	10		x		
Primula	10				
Rubus	10		x	x	
Syringa	10				

[a]Comba et al. (1999a,b); Corbet et al. (2001)

[b]Frankie et al. (2005, 2009); Pawelek et al. (2009)

[c]Tommasi et al. (2004)

[d]Garbuzov & Ratnieks (2014a,b)

Lists can raise public awareness.

For whatever reason, lists per se appear to be very attractive to the public. Lists of the fastest cars, the best rock songs, the scariest horror movies, top universities, or just about anything abound in the popular media, including the press, books, magazines, television, and, of course, the Internet. Therefore, lists of plants recommended to help pollinators via gardens are in a good position to raise awareness, educate, and enthuse a very large audience. As long as future lists state their limitations and encourage their readers to think for themselves and outside the confines of the list, they can be useful tools in communication from scientists to gardeners and conservationists.

Can garden plants really help mitigate pollinator declines?

When sympathetic gardeners select pollinator-friendly plants for their gardens, their main motivation is to help bees, butterflies, and other insect flower visitors by providing nectar and pollen for forage. But are garden plants really beneficial? The putative benefits of garden plants rest on the assumption that pollinating insect populations are limited by the available forage. Indeed, floral resource limitation is thought to be a major driver of the population abundance and diversity of wild bees, which are often positively correlated (reviewed in Roulston & Goodell, 2011). In a landmark study, Biesmeijer *et al.* (2006) showed that both bees and hover flies have declined in parallel with insect pollinated plants in both Britain and the Netherlands since 1980. Similarly, declines in floral abundance and diversity are blamed for the long-term decline of bumble bees (genus *Bombus*) in Europe (Goulson *et al.*, 2008b). Goulson *et al.* (2010) found that gardens are the land-use class that is most consistently positively correlated with bumble bee nest density and survival at a landscape-scale. Bumble bees have also declined dramatically in North America, but the causes in this region remain uncertain (Cameron *et al.*, 2011). In Germany, the abundance and richness of solitary bees and wasps are enhanced by mass-

flowering crops, which implies that floral resources are, indeed, a limiting factor (Holzschuh *et al.*, 2013; Diekötter *et al.*, 2014).

However, butterflies are, perhaps, not as easily helped by garden flowers. In a recent meta-analysis, Thomas *et al.* (2011) concluded that there was no evidence that populations of European butterflies are limited by any kind of adult resource, except for shelter. The most important factors influencing population size or trends were the quality of the larval habitat and the ability of adults to colonize new habitat patches. In Britain, a quarter of the resident butterfly species are limited by climate (Warren *et al.*, 2001). This may not be good news for butterfly lovers, but there is probably no harm in attracting butterflies to gardens. Butterflies are some of the most beautiful insects and, with the possible exception of the cabbage whiles, *Pieris rapae* and *Pieris brassicae*, are generally welcomed by gardeners and bring beauty, nicely complementing the buzz brought by the bees.

Chapter 4

No effect of patch size on insect visitation rate per unit area in garden-scale flower patches

Mihail Garbuzov, Andy Madsen, Francis L. W. Ratnieks

Abstract

Previous studies investigating the effect of flower patch size on insect flower visitation rate have compared relatively large patches (10-1000s m^2) and have generally found a negative relationship per unit area or per flower. Here, we investigate the effects of patch size on insect visitation in patches of smaller area (range c. 0.1-3.1 m^2), which are of particular relevance to ornamental flower beds in parks and gardens. We studied two common garden plant species in full bloom with 6 patch sizes each: borage (*Borago officinalis*) and lavender (*Lavandula* × *intermedia* 'Grosso'). We quantified flower visitation by insects by making repeated counts of the insects foraging at each patch. On borage, all insects were honey bees, *Apis mellifera* (n = 5506 counts). On lavender, insects (n = 737 counts) were bumble bees, *Bombus* sp., (76.9%), flies (22.4%), and butterflies (0.7%). On both plant species we found positive linear effects of patch size on insect numbers. However, there was no effect of patch size on the number of insects per unit area or per flower and, on lavender, for all insects combined or only bumble bees. The results show that it is possible to make unbiased comparisons of the attractiveness of plant species or varieties to flower-visiting insects using patches of different sizes within the garden scale range studied and make possible projects aimed at comparing garden plant varieties using existing garden patches of flowers of variable area.

Introduction

The effect of flower patch size on flower-visiting insects has been studied in fragmented natural (e.g. Dauber *et al.*, 2010) and agricultural settings (e.g. Cresswell & Osborne, 2004) in relation to gene flow and plant fitness (i.e. seed set and crop yield). These studies typically involved relatively large patches, ranging from tens to thousands of square metres, and generally found that insect visitation rate per unit area or per flower declined with patch size (Goulson, 2000 and references therein; Carvell *et al.*, 2011) or was weakly affected or unaffected (Walters & Stiles, 1996; Heard *et al.*, 2007; Dauber *et al.*, 2010).

Here, we examine the effects of patch size on insect flower visitation rate on a much smaller scale, using a range of patch sizes, c. 0.1-3.1 m^2 that are of particular relevance to ornamental flower beds in parks and gardens. Our null hypotheses (H_0) were that there is no relationships between (i) the number of flower-visiting insects foraging in a patch of flowers and (ii) the number per unit area with the total patch area. Many cultivated garden plants are attractive to flower-visiting insects and these are often recommended to gardeners to help bees and butterflies (e.g. Frankie *et al.*, 2009; RHS, 2011). But there is a need to determine the best plants in a more rigorous manner (Comba *et al.*, 1999a,b; Pawelek *et al.*, 2009; Chapter 5: Garbuzov & Ratnieks, 2014a). Understanding nature of the relationship between flower patch size and insect visitation is an important step in doing this, as it will allow the attractiveness of different varieties to be compared when grown in gardens and parks, and also in the wild, where patch size is not standardized.

Methods

Experimental setup and procedure

We studied two common garden plants attractive to flower-visiting insects: borage, *Borago officinalis* and lavender, *Lavandula* × *intermedia* 'Grosso'

To study borage, plants were grown from seed and potted on to 10 L pots each containing one large plant in full flower growing in standard potting compost (Nursery Stock, Sinclair). The following patch sizes and replicates were used: n = 5 patches × 1 pot (0.11 m^2), 3 × 2 pots (0.18 m^2), 2 × 4 pots (0.33 m^2), 2 × 8 pots (0.72 m^2), 1 × 16 pots (1.40 m^2) and 1 × 32 pots (3.13 m^2) (Fig. 4.1a). More patches of smaller than of larger sizes were set up in an attempt to counteract the greater variance in the smaller patches, as they are more strongly affected by stochasticity in insect arrivals and departures from a patch. Pots were arranged in such a way that plants in the same patch just touched to make a continuous patch. The patches were set up on the University of Sussex campus and monitored for 3 days (28-30 September 2011) in one location and for 3 days (2-4 October 2011) in another location 430 m away to ensure that our results are more general and not strongly location or time specific. Patches were all in the same area but with gaps of 2 m between patches, thereby mimicking the way plants are grown in garden flower beds. On each day, the pots were reallocated among patches after first counting the number of flowers per pot. This was to make the number of flowers per patch reflect, as much as possible, the number of plants, and to avoid the possibility that particular plants with above-average numbers of flowers caused a systematic bias to certain plots by being more attractive. Counts were made only on warm sunny days with no strong wind and no rain,

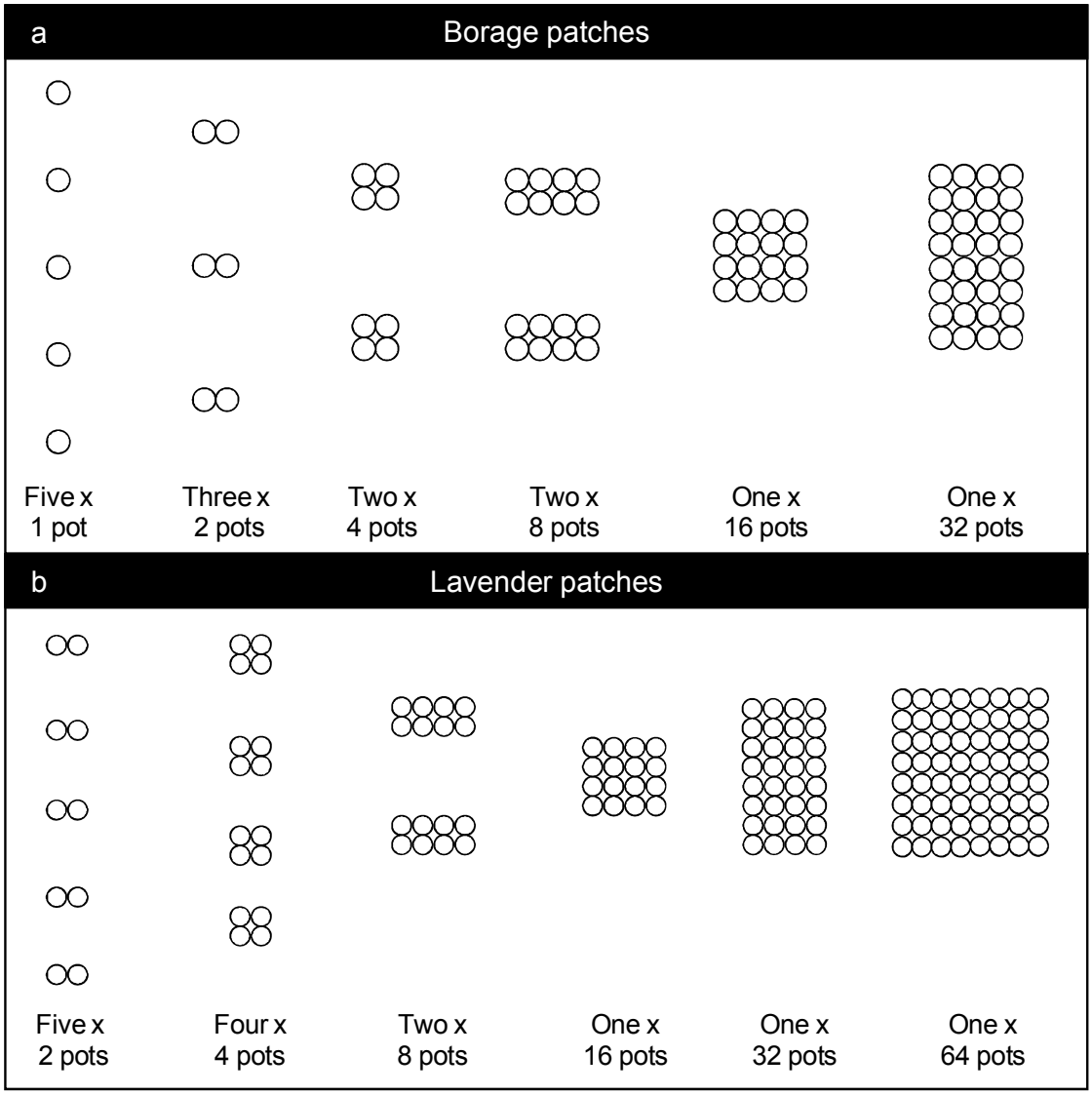


Figure 4.1. Diagram showing the numbers of patches and the arrangement of pots within patches used in the experiments with (a) borage and (b) lavender. Each circle represents one pot with one plant. The arrangement of patches is conceptual, not to scale and does not represent the actual arrangement used in the experiments.

i.e. when all flower-visiting insect categories could be active. Flower visitation was quantified by making repeated counts. At each count, the number of foraging insects in a patch was recorded near instantaneously (<10 s) by eye. In the largest patches, c. 2.6-3.1 m^2, the highest numbers of foraging insects in one count were 11 insects in the borage experiment and 7 in the lavender experiment. This was near the limit of what can be quantified accurately using the methodology of near-instantaneous snapshot counts. In future research, if plots are too large or have too many insects to count at one time, a patch could be subdivided and counted in sections.

On each day, 70 counts were taken from each patch. Counts were made in groups of 10, in which patches were observed sequentially, making one count from one patch at a time. Each group of 10 counts per patch was made within a period of c. 15-20 minutes. These groups of counts were separated by 30-minute breaks. Since some pseudoreplication may occur due to counting the same insect on the same patch visit, each group of 10 consecutive counts was averaged to give 7 count-group means per patch per day for use in the statistical analyses. Although the same insects may have been recorded in different count-groups, the data still represent independent patch choices given the 30-minute gaps between groups of counts.

To study lavender, plants were purchased from Downderry Nursery (Hadlow, Kent, UK), a lavender specialist and potted on to 3 L pots, each containing one large plant in full flower growing in standard potting compost (Nursery Stock, Sinclair). Lavender was studied in only one location on the University campus, which was the same location as the second borage location. A second trial was not carried out as the borage data have shown no significant difference between the two locations (see below in Results). The following patch sizes were used: n = 5 patches × 2 pots (0.08 m^2), 4 × 4 pots (0.16 m^2), 2 × 8 pots (0.32 m^2), 1 × 16 pots (0.64 m^2), 1 × 32 pots (1.28 m^2) and 1 × 64 pots (2.56 m^2) (Fig. 4.1b). In total, 100 counts were taken from each patch over 2 days (30-31 August 2012) when the plants were near full bloom. As in the experiment using borage, groups of 10 counts were averaged to a single mean, yielding 10 count-group means in total from each patch. The number of open flowers (in lavender sometimes termed 'florets') was also counted in each patch.

Statistical analyses

We used Generalized Linear Mixed Models (GLMMs) (Zuur *et al.*, 2009) to test the relationships between the response variables, which included (i) mean number of insects per count-group, (ii) mean number of insects per count-group per unit area and (iii) mean number of insects per count-group per flower, and the fixed variables, which

included (i) patch area and (ii) number of open flowers in a patch. Experiment location (borage) and patch (both borage and lavender) were included as random factors to account for possible non-independence of data within locations and different patches of the same size. As the number of flowers per patch was highly colinear with patch area, only one of these fixed variables was included in a model at a time. In models where there was an empirical reason to predict a relationship going through the origin (e.g. the number of insects on patches of zero area cannot be positive), we tested the significance of intercept ≠ 0 at α=0.05. In cases where it was not significant, we fitted final models assuming intercept = 0. GLMMs were fitted by maximum likelihood using function *lme* (package *nlme* v.3.1-109, Pinheiro *et al.*, 2013) in R v.3.0.0 (R Development Core Team, 2012). The significance of terms was determined using full-model t-tests, as suggested by (Whittingham *et al.*, 2006).

Results

On borage all flower-visitors were honey bees (*Apis mellifera* L., n=5506 counts). On lavender the flower-visitors were 76.9% bumble bees (*Bombus* spp., n=567), 22.4% flies (Diptera, n=165) and 0.7% butterflies (*Maniola jurtina* L., Lepidoptera, n=5). In most cases, it is not possible to identify bumble bees and flies to the species on the wing. However, it is possible to identify British bumble bees to narrow groups of species based on the colour banding pattern, where each group is typically represented by one or two common species (Fussell & Corbet, 1992). On this basis, 13.2% of the bumble bees were 'two-banded white tails' (main species *B. terrestris/lucorum*), 4.1% 'three-banded white tails' (main species *B. hortorum*), 77.6% 'browns' (main species *B. pascuorum*), 4.8% 'banded red tails' (main species *B. pratorum*) and 0.4% 'black-bodied red tails' (main species *B. lapidarius*). Due to low numbers recorded in some groups, the response of bumble bees to patch size was analysed collectively for the genus, rather than separately for each species group.

The mean number of insects per count-group was significantly related to patch area in both borage (t=25.30, df=82, P<0.001) and lavender (bumble bees: t=25.36, df=13, P<0.001; all insects: t=26.71, df=13, P<0.001) (Fig. 4.2a-c). Furthermore, the constant linear slopes in Fig. 4.2a-c show that the mean numbers of insects per count-group per unit area were not affected by patch area in borage (t=-1.30, df=81, P=0.198) and lavender (bumble bees: t=1.42, df=12, P=0.180; all insects: t=1.53, df=12, P=0.153) (Fig. 4.2d-f).

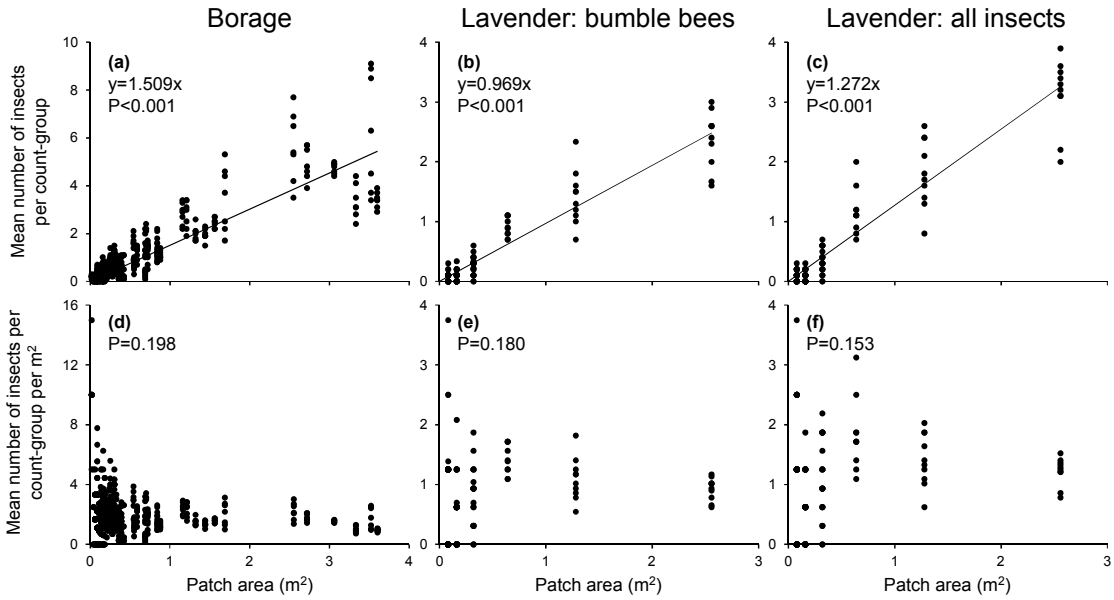


Figure 4.2. Effect of patch area on the mean number of foraging insects per count-group (a-c) or the mean number per m^2 (d-f). On borage, *Borago officinalis* all insects were honey bees (n=588 count-groups). On lavender, *Lavandula* × *intermedia* 'Grosso' 76.9% were bumble bees, 22.4 % flies, 0.7 % butterflies (n=140 count-groups). A count-group is a group of 10 counts taken in quick succession. Regressions lines in a-c were fitted through the origin.

As the number of flowers per patch was highly colinear with patch area (borage: Pearson's r = 0.985, P<0.001; lavender: r=0.983, P<0.001), the relationship between the mean number of insects per count-group with patch area was presumably driven primarily by the number of flowers per patch. In all cases, the mean number of insects per count-group was positively related to the number of open flowers in a patch (borage: t=29.74, df=82, P<0.001; bumble bees on lavender: t=39.03, df=12, P<0.001, all insects on lavender: t=37.43, df=12, P<0.001) (Fig. 4.3a-c). However, the mean number of insects per count-group per flower was not affected by patch area (borage: t=-0.78, df=81,

P=0.436, bumble bees on lavender: t=1.77, df=12, P=0.102, all insects on lavender: t=2.06, df=12, P=0.061) (Fig. 4.3d-f).

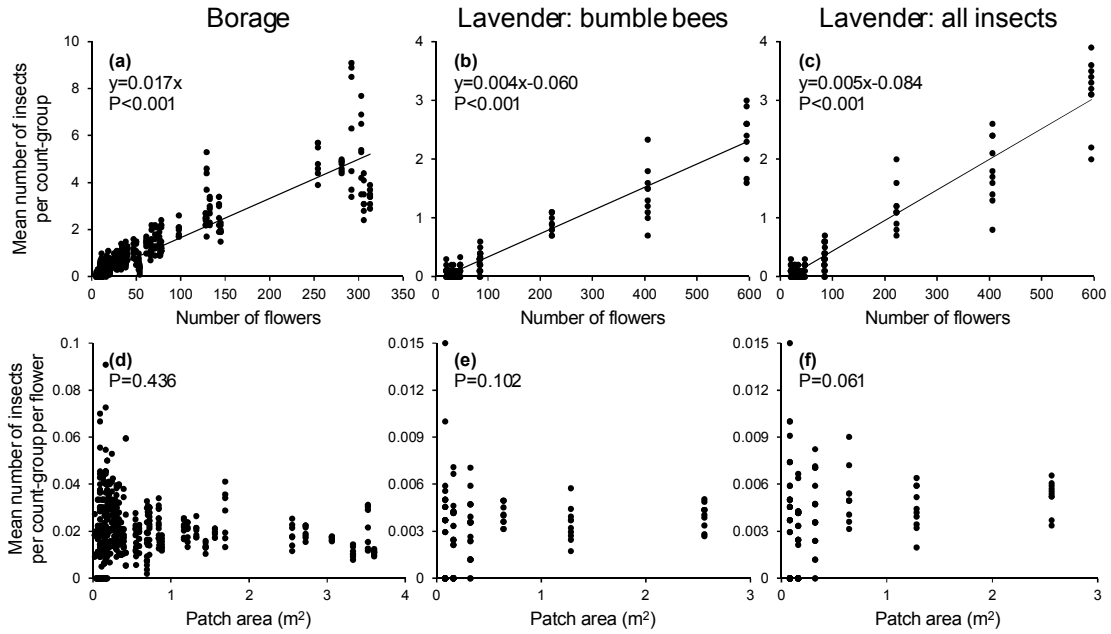


Figure 4.3. Effect of the number of open flowers per patch on number of foraging insects (a-c) and the effect of patch area on the number of insects per flower (d-f). On borage, *Borago officinalis* all insects were honey bees (n=588 count-groups). On lavender, *Lavandula* × *intermedia* 'Grosso' 76.9% were bumble bees, 22.4 % flies, 0.7 % butterflies (n=140 count-groups). A count-group is a group of 10 counts taken in quick succession. In (a), the intercept was not significantly different from zero, hence the regression line was fitted through the origin. In (b-c), the intercept was retained.

Inclusion of location as a random factor did not significantly improve the fit of the borage model (Likelihood-ratio test, L=2.29, df=1, P=0.130). However, inclusion of patch improved the fit of both borage (L=261.64, df=1, P<0.001) and lavender (bumble bees: L=12.32, df=1, P<0.001; all insects: L=9.83, df=1, P=0.002) models.

Discussion

In both borage and lavender, the number of foraging insects per patch was positively linearly related to patch area, which was itself highly correlated with number of flowers. This suggests that insects foraging on patches of both plant types were distributed in an "ideal free" way, i.e proportional to the amount of resources available in each patch (Dreisig, 1995). In contrast to some previous studies that investigated patches of greater size (Walters & Stiles, 1996; Goulson, 2000 and references therein; Heard *et al.*, 2007;

Dauber *et al.*, 2010; Carvell *et al.*, 2011), there was no tendency for the larger patches to have fewer insects per unit area or per flower. This was, presumably, because the patch sizes we studied were all small in relation to insect movement so that unvisited flowers and inflorescences were almost equally easy to locate in both large and small patches (Goulson, 2000). In addition, the patterns we observed are consistent with the absence of edge effects, as the differentiation of a patch into edge and interior from an insect perspective may only occur above a certain patch size (Burgess *et al.*, 2006).

Our results are very encouraging in terms of quantifying the relative attractiveness of garden plants to flower-visiting insects, with the aim of helping to determine which varieties are most insect-friendly. Thus, in our data, the slope estimates of the relationship between the number of insects counted and patch area (Fig. 4.2a,c; m = 1.509 for borage and 1.272 for lavender) show that borage was c. 18% more attractive to insects than lavender, although the species composition of flower-visitors was markedly different. However, these data pertain only to the peak bloom and take no account of the length of the flowering period. In another study comparing the attractiveness of plant varieties grown in patches of the same size, 1 m^2, which followed the plants for most of their flowering period in two seasons, borage attracted, on average, 2.48 insects per count per m^2 versus 1.94 for *L.* × *intermedia* 'Grosso', or greater by c. 28% (Chapter 5: Garbuzov & Ratnieks, 2014a). Our results open up a way for 'citizen science' in which members of the public can count insects in existing patches of garden plants that are grown in parks or gardens in patches of different area, as it is possible to determine the attractiveness of plants to flower-visiting insects in terms of the number of insects counted per unit of flower patch area.

Chapter 5

Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects

Mihail Garbuzov, Francis L. W. Ratnieks

Abstract

Pollinating insects are globally declining, with one of the main causes being the loss of flowers. With the value of countryside reducing, urban areas, particularly gardens, are increasingly recognized as of benefit to wildlife, including flower-visiting insects. Many gardeners specifically select plant varieties attractive to wildlife. Given the wide public interest, many lists of recommended varieties have been produced by both amateurs and professional organizations, but appear not to be well grounded in empirical data. These lists, however, are not without merit and are an obvious starting point. There is clearly a need to put the process onto a firmer footing based more on data and less on opinion and general experience. We collected data over two summers by counting flower-visiting insects as they foraged on 32 popular summer-flowering garden plant varieties in a specially planted experimental garden, with two smaller additional gardens set up in year two to check the generality of the results. With many thousands of plant varieties available to gardeners in the UK, and other countries or regions, it would have been an impossible task to make a comprehensive survey resulting in a complete and authoritative list. Our results, however, are valuable and encouraging. Garden flowers attractive to the human eye vary enormously, approximately 100-fold, in their attractiveness to insects. Insects, especially bees and hover flies, can be attracted in large numbers with clear differences in the distribution of types attracted by different varieties. Our results clearly show that there is a great scope for making gardens and parks more bee- and insect-friendly by plant selection. Horticulturally modified plant varieties created by plant breeding, including hybrids, are not necessarily less attractive to insects and in some cases are more attractive

than their wild-type counterparts. Importantly, all the plants we compared were considered highly attractive to humans, given that they are widely sold as ornamental garden plants. Helping insect pollinators in gardens does not involve extra cost or gardening effort, or loss of aesthetic attractiveness. Furthermore, the methods of quantifying insect-friendliness of plant varieties trialled in this study are relatively simple and can form the basis of further research, including 'citizen science'.

Introduction

Global biodiversity is in decline (Barnosky *et al.*, 2011). Pollinating insects are no exception, with the main factor being loss of flowers, driven primarily by human activities, such as development and agricultural intensification, which lead to habitat loss and degradation (Goulson *et al.*, 2005; Biesmeijer *et al.*, 2006; Potts *et al.*, 2010a). With the wildlife value of the countryside reducing, the value of urban areas is increasingly being recognized (Frankie & Ehler, 1978; Cane, 2005; Dearborn & Kark, 2010; Sanderson & Huron, 2011). High species diversity has been recorded in urban green spaces, such as parks and gardens (Helden & Leather, 2004; Matteson *et al.*, 2008; Owen, 2010), with private gardens often being the largest and probably the most important component (Goddard *et al.*, 2010). In the United Kingdom, 87% of households are associated with a garden (Davies *et al.*, 2009) and gardening is a popular hobby (Taylor, 2002). In addition, many gardeners are supportive of wildlife, with most UK gardeners (74–78%) engaging in some form of 'wildlife gardening'. That is, doing something to attract or encourage wildlife (Good, 2000), including the 31% who select plants attractive to wildlife or the 66% who feed birds in their garden (Mew *et al.*, 2003; DEFRA, 2007).

Garden plants are often non-native, and this may reduce their usefulness to some wildlife. For example, many herbivorous insects have a narrow range of suitable food plants (Novotny & Basset, 2005; Dyer *et al.*, 2007). However, this does not prevent them from being useful to flower-visiting insects seeking nectar and pollen, as these are general

resources. Nectar, for example, is mainly sugar and water (Nicolson & Thornburg, 2007), and so it is edible whether from a native or a non-native plant. Many garden plants have also been bred to alter their appearance, such as by the 'doubling' of petals, which may reduce floral rewards or their accessibility (Comba *et al.*, 1999b; Corbet *et al.*, 2001).

Given the public interest in helping wildlife, a large number of recommended plant lists have been produced, by both amateurs (e.g. Baines, 2000; Lavelle & Lavelle, 2007) and professional organizations (RHS, 2011; Xerces Society, 2011). However, these appear not to be well grounded in empirical data. For example, Thompson (2006) referred to one list of wildlife friendly plants produced by Natural England, a government-funded agency responsible for protection and improvement of the natural environment, as 'looks very much as if it was put together late one Friday afternoon'. In addition, lists of bee- and butterfly-friendly plants vary greatly even when they are for the same country, suggesting that the underlying information is based mainly on personal observations, experience, opinion and, perhaps, uncritical recycling of earlier lists (Chapter 3).

Lists of bee- and butterfly-friendly plants are not without merit and are an obvious starting point for determining which plants are good for flower-visiting insects. However, there is a need to put the process onto a firmer footing based more on data and less on opinion and general experience. This study is an attempt to do this. We collected data over two summers in which flower-visiting insects were counted as they foraged on 32 popular garden plant varieties in a specially planted experimental garden. In addition, two smaller gardens were set up in year two to check the generality of the results. With many thousands of plant varieties available to gardeners in the UK, it would have been an impossible task to make a comprehensive survey resulting in a complete and authoritative list. What our data do show, however, is valuable and encouraging. Garden flowers attractive to the human eye vary enormously, approximately 100-fold, in their attractiveness to insects. This shows that plant selection can make a great difference in the value of gardens and parks to flower-visiting insects, and at no additional cost. Insects, and especially bees, can be attracted in large numbers with clear differences in the distribution of types attracted by different garden plant varieties.

Methods

Experimental plant varieties and flower beds

We studied 32 garden plant varieties that include 19 species and hybrids, both native and exotic to Britain, with particular focus on varieties of lavender (*Lavandula* spp.), as it is known to be attractive to bees (Pawelek *et al.*, 2009); for full list see Appendix 5.1. Varieties were selected based on the following three criteria: they were (i) popular as garden plants in their own right due to their attractive flowers or foliage (e.g. Lamb's ear, *Stachys byzantina*), (ii) widely and easily available for purchase and (iii) flowered mainly or exclusively in late summer, July and August, as these are the months when honey bee foraging distances in the same area are greatest (Couvillon *et al.*, 2014a), indicating challenging foraging conditions and, therefore, the period when garden flowers can be particularly beneficial to flower-visiting insects.

The main experimental flower bed was on the University of Sussex campus (lat: 50.865646, long: -0.090771943) on chalky soil of the South Downs. All 32 varieties were planted in 1 × 1 m patches, two patches per variety, in two concentric circles (inner diameter 12.2 m, outer 19.2 m), with one variety per circle in a random position (Fig. 5.1). There were gaps of c. 0.5 m (inner) and 1.0 m (outer) between adjacent patches within the same circle and 1.5 m between the circles. This arrangement was chosen to eliminate any edge effects, which might have affected insect visitation. Data were collected in both 2011 and 2012.

Additionally, to ensure our results were not location specific, for example, due to local soil conditions or insect abundance, 13 of the 32 varieties (Appendix 5.1) were planted at two additional locations in 2012. This subset was chosen to confirm certain notable trends seen in the data at the end of the first season (2011). For example, *Borago* was mostly visited by honey bees, while *Lavandula* mostly by bumble bees. *L.* × *intermedia* received more insect visits than *L. angustifolia*, while sharp colour contrast (traditional

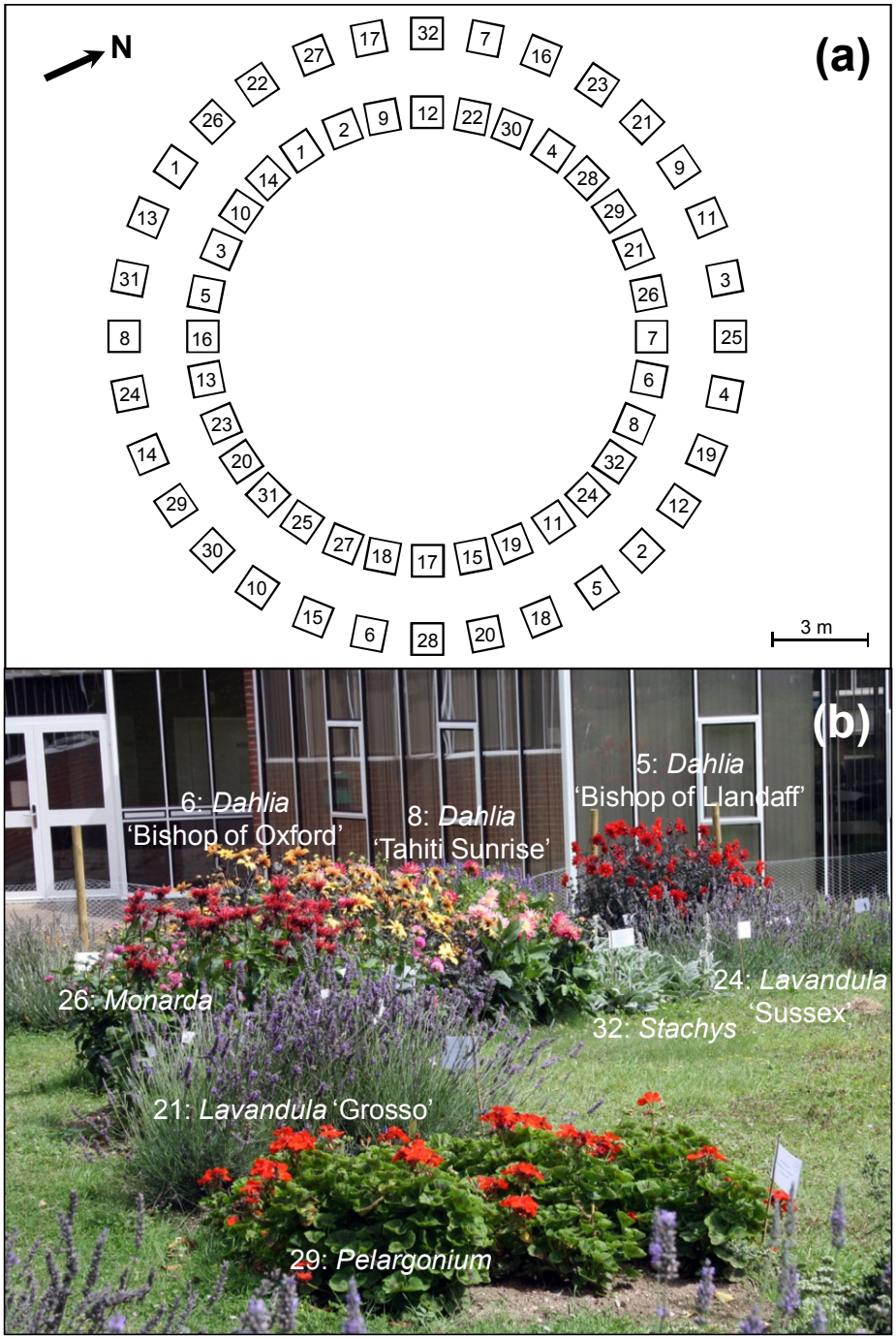


Figure 5.1. (a) Schematic layout of the experimental flower garden on the University of Sussex campus, showing the two concentric circles, each consisting of 32 1 × 1 m flower patches. Numbers correspond to the varieties, as listed in Appendix 5.1. (b) Photograph showing a section of the inner circle, taken in August 2011 when most varieties were in full bloom.

blue/purple *vs*. white or pink) had no effect on the number of visits. Open-flowered *Dahlia* varieties were more attractive than those with more modified flower forms. *Origanum* and *Stachys* seemed to have disproportionately large numbers of visits by 'other' wild bees, while *Erysimum* was most attractive for butterflies and moths. One location was 4.5 km away at Plumpton College (lat: 50.905665, long: -0.074753791) where

the soil is also chalky, and the other 26.3 km away in FR's private garden in Magham Down (lat: 50.880426, long: 0.28488247), where the soil is sandy. Only one 1 × 1 m patch per variety was planted, and the patches were arranged in a line with 30 cm gaps.

Perennials were bought in pots from nurseries and garden centres and planted in June 2011 (University of Sussex) and May-June 2012 (Plumpton College & Magham Down). Borage (*Borago officinalis*), which is an annual, was sown in May each year to give peak flowering in July–August. Viper's bugloss (*Echium vulgare*) is a biennial, flowering in the second year of its life cycle. However, we were able to induce flowering in the first year by keeping young seedlings in a greenhouse at 24:0 light/dark photoperiod for 8 weeks before transplanting them to patches in the flower bed. The non-hardy anise hyssop (*Agastache foeniculum*) and geranium (*Pelargonium* × *hortorum*) were dug out at the end of 2011 season, overwintered in a heated greenhouse and replanted in May 2012. The four *Dahlia* varieties, which are also non-hardy, were grown from tubers in a greenhouse starting in March each year and planted out 8 weeks later. Prior to planting, all patches were fertilized with multipurpose organic fertilizer (Fish, Blood & Bone, Sinclair) and controlled release fertilizer (Sincrocell 9, Sinclair). Appendix 5.1 gives the suppliers of each plant variety.

Plant and patch characteristics

In each patch, an appropriate number of plants were planted according to their size (Appendix 5.1) such that the patch was nearly fully covered, but allowing for some further growth. Plants were trimmed as necessary to ensure that they did not overgrow the patch perimeter. In some cases, slow growth or plant death (only in *E. vulgare* at the University of Sussex) resulted in patches that were not covered completely. To allow for <100% plant cover, on each day of data collection, patches were photographed from above to determine plant cover using ImageJ 1.45s software (National Institute of Health, USA).

On each day of data collection, the bloom intensity of patches was quantified by assigning a score 0 (absence of bloom), 1 (<⅓ of maximum), 2 (⅓–⅔ of maximum) or 3

(full bloom, >⅔ of maximum; after Anderson & Hubricht 1940) and included as a covariate in the analyses. In addition, as corolla length is known to influence the type of flower-visitors and their ability to gather nectar (Balfour *et al.*, 2013), it was estimated in each variety by measuring 20 non-systematically selected flowers (10 from each patch at bloom intensity 2 or 3) to the nearest 0.1 mm using digital callipers.

Recording insect flower-visitors

In the main flower bed at the University of Sussex, insects visiting the flowers were counted on 13 days from 14 July to 7 October 2011 and 12 days from 29 June to 18 September 2012. Counts were made only on days with favourable weather. That is, based on our experience, the combination of sunlight, temperature and wind was such as to allow all insect categories to be active. Counts were made at approximately weekly intervals throughout the main flowering period of most plant varieties (Appendix 5.2). In addition, insects were recorded on 6 days from 18 August to 18 September 2012 at Plumpton College and on 8 days from 9 August to 10 September 2012 at Magham Down.

The number of insect flower-visitors on each patch was quantified using 'snapshot' counts, in which the number of foraging insects was determined near instantaneously (<10 s) by eye. This 'snapshot' count method was chosen over other possible methods, such as counting the number of insects arriving at a patch in a defined time interval, as it is quick to implement and therefore practical for assessing many patches. In the main flower bed at the University of Sussex, one count was taken from each patch at hourly intervals between 9:30 and 16:30 BST, yielding eight counts per patch per day. In the two additional flower beds, 10 counts per patch were taken per day, typically during a c. 2-h period. As insects generally remained on the same patch for only a few minutes during a foraging trip, the 60-min intervals between counts meant that the same insect was unlikely to have been counted twice on the same patch visit. Thus, the data represent independent foraging choice decisions even though individual insects may make multiple visits to the same patch. Even when multiple visits by the same insect to

the same patch do occur, this shows a real preference rather than the mere persistence of the same insect at the same patch during a single patch visit.

The insects counted in the snapshots were identified and grouped to taxa as follows: (1) honey bees (*A. mellifera*), (2) two-banded white-tailed bumble bees *(Bombus terrestris/lucorum* group, after Fussell & Corbet (1992)), (3) three-banded white-tailed bumble bees (*Bombus hortorum* group), (4) brown bumble bees (*Bombus pascuorum* group), (5) other bumble bees, (6) other bees (non-Apis and non-Bombus), (7) hover flies (Diptera: Syrphidae), (8) butterflies and moths (Lepidoptera) and (9) all other insects. Additionally, Lepidoptera (group 8) were identified to species, other bees (groups 5, 6) and other insects (group 9) to species or other taxonomic ranks, as appropriate. However, they were grouped in analyses due to the low numbers of individual species or subgroups in the datasets (Table 5.1, Fig. 5.2). The levels of identification used were appropriate given the counting method, in which insects were identified as they foraged and were not collected. In practice, this meant that most insects (87–92% per dataset) other than flies, Diptera, were identified to species or to groups of species that could easily be separated in the field (e.g. the different bumble bee subgroups).

Statistical analyses

The number of insects per snapshot was divided by plant area cover to form the response variable in the analyses. This is justifiable, because the number of insects per snapshot is linearly related to the area (Chapter 4). All statistical analyses were performed in R v.3.0.0 (R Development Core Team, 2013). Prior to analyses, the data were explored as advised by (Zuur *et al.*, 2010). General linear models (GLMs; function *gls*, package *nlme*, Pinheiro *et al.*, 2012) were used to examine the relationships between the response variable, plant variety, bloom intensity and mean corolla length as main fixed effects. No interactions were modelled, as they were not part of the a priori hypotheses to be investigated. The dataset was 'collapsed' by averaging out across the two patches of each plant variety, and also within each day, by taking daily means. Further, to account for temporal

autocorrelation within the data recorded at approximately weekly intervals across the season, the AR-1 correlation structure was added to the models (Zuur *et al.*, 2009). One model was fitted for each insect group in both the 2011 and 2012 University of Sussex datasets. The significance of P-values was judged against the Bonferroni-corrected α-level (0.05 divided by the number of models per dataset). As plant variety and mean corolla tube length were highly correlated (i.e. each variety had a different mean length), only one of these variables was included in a model at a time. The significance of terms was determined using F-tests on a full model, which is appropriate, because the main aim was to analyse the significance of terms, rather than to use the models predictively (Whittingham *et al.*, 2006). *Post-hoc* pairwise comparisons of plant varieties were performed using Tukey's HSD test (function *glht*, package *multcomp*, Hothorn *et al.*, 2008).

Consistency among datasets was tested using Spearman's rank correlation test. This is more appropriate than a parametric correlation test, because consistency in rank is both more conservative and more relevant to the underlying aim of the test than consistency in the absolute numbers of insects attracted, which may vary among years and locations. All other relationships (in the attractiveness of plant varieties among different insect flower-visitor groups) were tested using Pearson's correlation test (function *cor.test* for all correlation tests).

Results

Attractiveness of plant varieties to insect flower-visitors

The relative abundance of insect groups at the University of Sussex is shown in Fig. 5.2. Across the 2 years, over 84% of insects recorded were bees, comprising 47–62% *Bombus* spp., 26–32% *A. mellifera* and 3–5% other bee species. Hover flies were 7–10%, butterflies and moths 1–3% and other insects 1–3%. Further taxonomic breakdowns of these groups

are given in Table 5.1. The mean number of insects per count per m^2 was significantly affected by plant variety in most main insect groups (Appendix 5.3). Bloom intensity (covariate) was also significant in most models (Appendix 5.3). The length of flower corolla tube was a significant predictor in only a few models (Appendix 5.3). However, the slope estimates of relationships were close to zero (0.01–0.04), making these relationships of little importance. The results of *post-hoc* Tukey's HSD tests comparing plant varieties are shown in Fig. 5.3. Due to the very large numbers of pairwise comparisons, the test had low power to differentiate between varieties. Nevertheless, it was sufficient to reveal the broad picture.

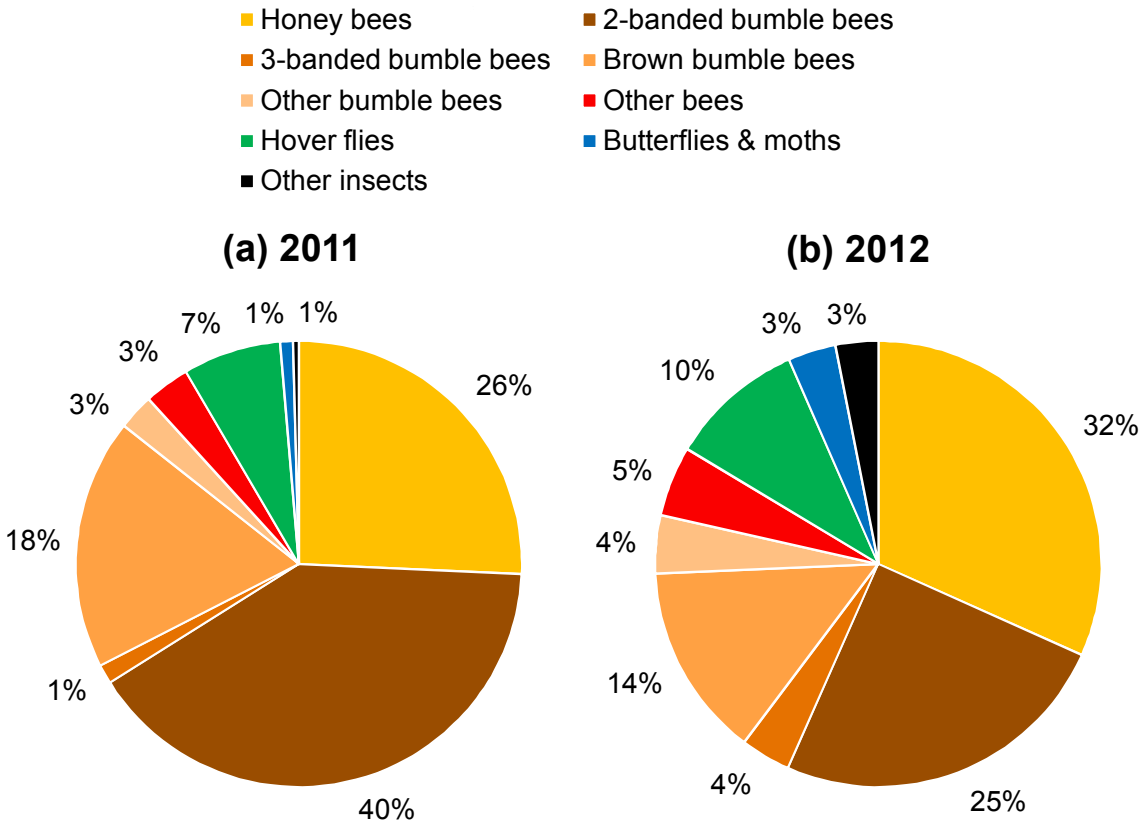


Figure 5.2. Relative abundance of insects in nine main groups recorded in the 2 years at the University of Sussex in 2011 (a) and 2012 (b). More detailed taxonomic breakdowns of other bumble bees, other bees, butterflies & moths, and other insects are given in Table 5.1.

Table 5.1. Breakdown of main insect groups that were grouped together in the analyses.

	Common name	University of Sussex 2011	University of Sussex 2012	Plumpton College 2012	Magham Down 2012
Other *Bombus* groups					
Black-bodied red tails		12%	20%	-	45%
Banded red tails		84%	78%	100%	7%
Unidentified		4%	2%	-	48%
Other bees					
Anthidium manicatum	Wool-carder bee	Not identified	95%	100%	100%
Unidentified		Not identified	5%	-	-
Lepidoptera					
Butterflies					
Aglais urticae	Small tortoiseshell	3%	10%	-	38%
Aphantopus hyperantus	Ringlet	-	1%	-	-
Gonepteryx rhamni	Brimstone	-	1%	-	-
Inachis io	Peacock	-	1%	-	-
Lycaena phlaeas	Small copper	-	1%	-	-
Maniola jurtina	Meadow brown	22%	62%	71%	52%
Ochlodes sylvanus	Large skipper	2%		-	-
Pieris brassicae	Large white	3%	1%	-	5%
Pieris rapae	Small white	34%	4%	29%	-
Polygonia c-album	Comma	3%	-	-	-
Polyommatus coridon	Chalkhill blue	2%	-	-	-
Polyommatus icarus	Common blue	-	9%	-	-
Pyronia tithonus	Gatekeeper	-	1%	-	-
Thymelicus sylvestris	Small skipper	2%	4%	-	-
Vanessa atalanta	Red admiral	3%	1%	-	-
Vanessa cardui	Painted lady	2%	-	-	-
Moths					
Autographa gamma	Silver Y	-	1%	-	5%
Macroglossum stellatarum	Hummingbird hawk-moth	22%	-	-	-
Pyrausta aurata	Mint moth	-	2%	-	-
Zygaena trifolii	Five-spot burnet	-	1%	-	-
Other insects					
Coleoptera	Beetles	20%	9.5%	11%	4%
Diptera	True flies	63%	90%	89%	92%
Vespula spp.	Yellowjacket wasps	17%	0.5%	-	4%

Bombus sub-groups follow Fussell & Corbet (1992). For absolute and relative abundance of groups see Fig. 5.2.

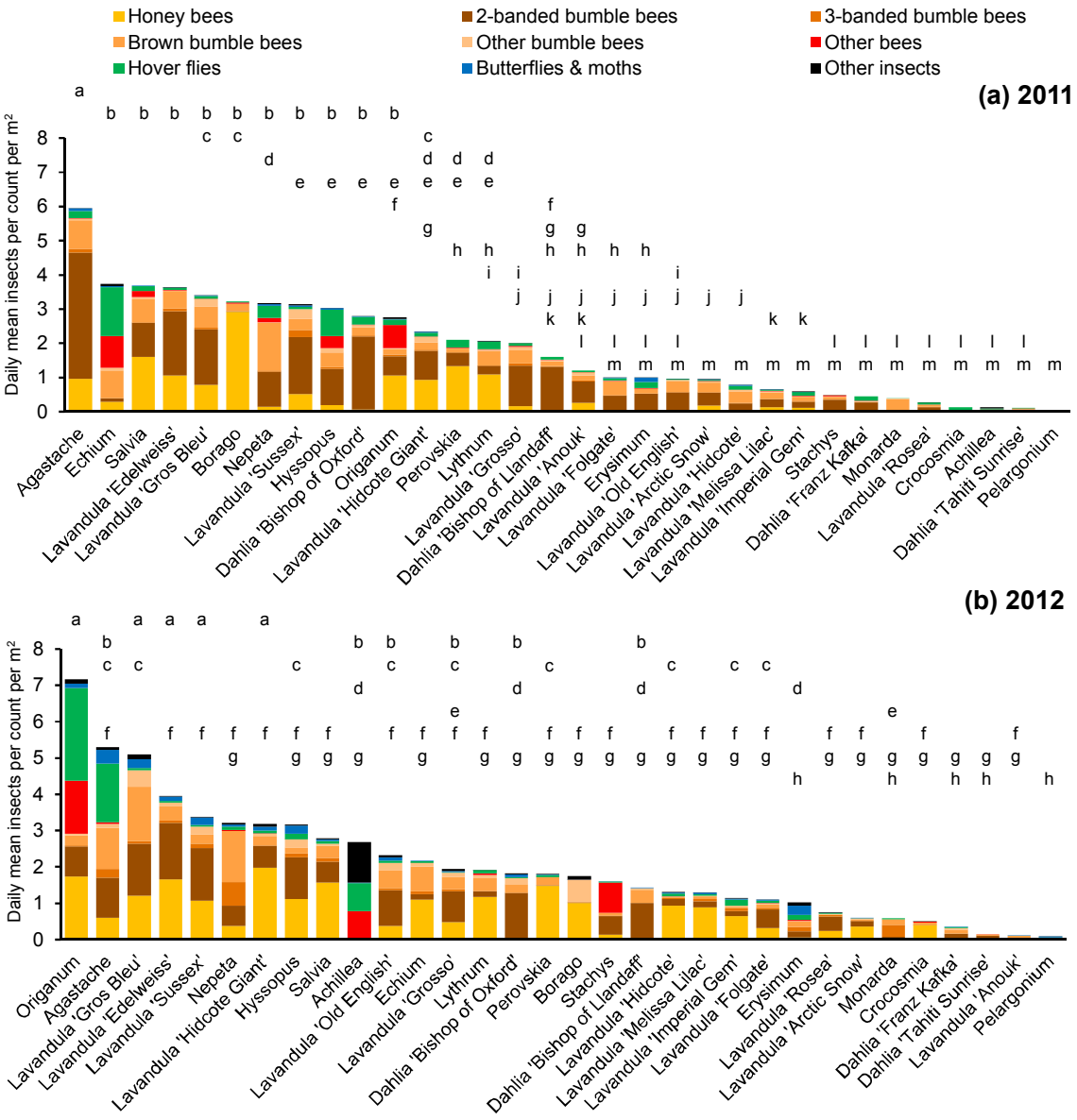


Figure 5.3. Daily mean numbers of insects per snapshot per 1 × 1 m patch recorded on 32 garden plant varieties at the University of Sussex in 2011 (a) and 2012 (b), Letters above bars represent significant differences based on Tukey's HSD test, where varieties sharing a common letter are not significantly different from each other at α = 0.05. Full plant names are given in Appendix 5.1.

Consistency among years and locations

The relative abundance of insect groups and plant variety attractiveness at Plumpton College and Magham Down in 2012 (Appendix 5.4) were similar to those recorded at the University of Sussex in both years. In addition, the mean number of insects per count per m^2 recorded on different varieties at the University of Sussex correlated highly between 2011 and 2012 (Spearman's correlation: $r_s = 0.754$, $S = 1343.62$, $P < 0.001$, Fig. 5.4a). The

numbers of insects per variety recorded at the University of Sussex in 2012 were also significantly related to those recorded at both Plumpton College (r_s = 0.650, S = 127.35, P = 0.016, Fig. 5.4b) and Magham Down (r_s = 0.791, S = 76.00, P = 0.002, Fig. 5.4b) flower beds. This suggests that the results are general, rather than being year or location specific.

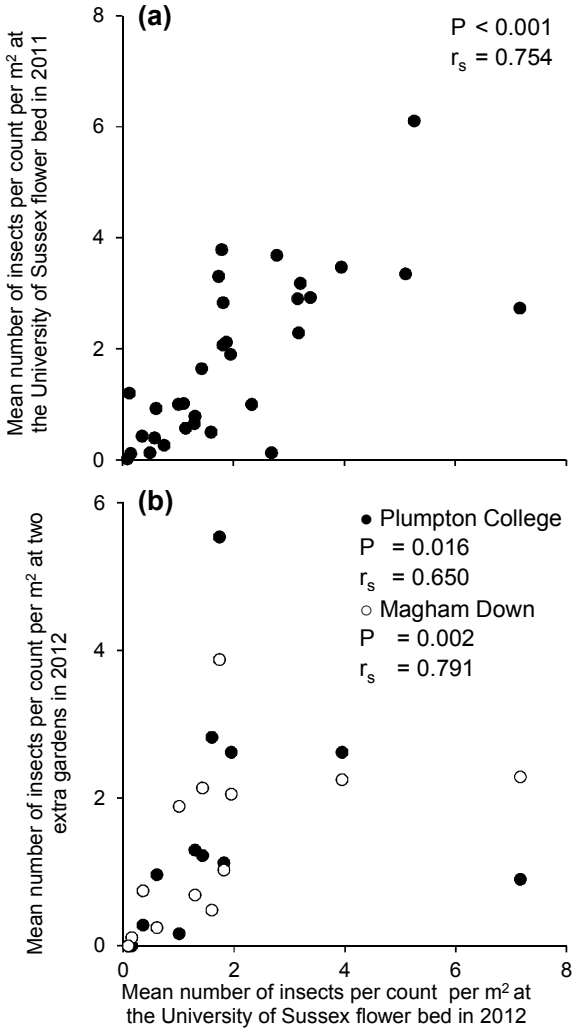


Figure 5.4. Correlations between the number of insects per count recorded on different plant varieties at the University of Sussex flower bed in 2012 with that in (a) 2011, and (b) the additional flower beds at Plumpton College (●) and Magham Down (○) in 2012.

Comparison of lavender varieties

Closer examination of lavender varieties showed that (i) not all varieties were equally attractive (GLM: F12,13 = 9.75, P < 0.001) and (ii) *L.* × *intermedia* as a group (mean ± SE = 2.91 ± 0.31 insects count^{-1} m^{-2}) were more attractive than both the *L. angustifolia* group (mean ± SE = 0.88 ± 0.09 insects count^{-1} m^{-2}) and *L. stoechas* (mean ± SE = 0.66 ± 0.54 insects count^{-1} m^{-2}; $F_{1,20}$ = 34.86, P < 0.001; Fig. 5.5a). However, the number of insects

attracted was not affected by either total bloom duration ($F_{1,20}$ = 3.52, P = 0.075; Fig. 5.5b) or corolla tube length ($F_{1,20}$ = 0.0004, P = 0.985). Honey bees and bumble bees together comprised the majority (mean 90%, range 73–97%) of flower-visitors on *Lavandula* varieties. The number of honey bees, as a proportion of honey bees and bumble bees together, varied considerably among varieties (range 11–55%). However, this was not consistent between 2011 and 2012 (r = 0.290, P = 0.337) and did not correlate with corolla tube length in 2011 (r = -0.199, P = 0.515), 2012 (r = 0.202, P = 0.508) or the mean of 2011 and 2012 (r = 0.094, P = 0.759).

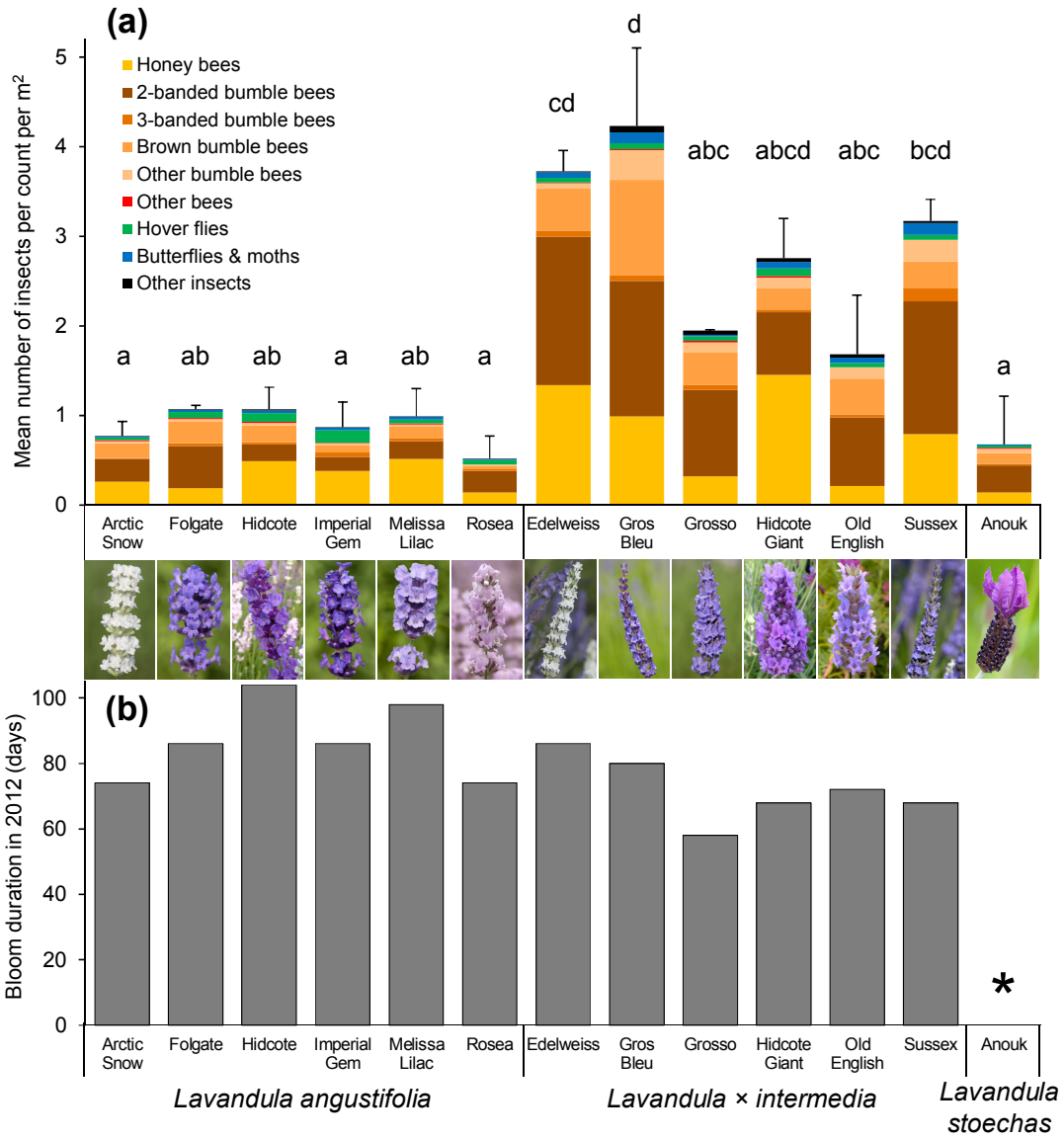


Figure 5.5. (a) Numbers of insects per count per m^2 on 13 *Lavandula* varieties. Bar heights are grand means of two datasets (University of Sussex 2011 & 2012) + SE. Letters above bars denote results of *post-hoc* Tukey's HSD pairwise comparison tests. (b) Total bloom duration of each variety in 2012, c. 15 months after planting out when plants were well established, thus showing natural phenology. **L. stoechas* 'Anouk' was in poor condition and did not reach full bloom in 2012. Photo credits: Simon Charlesworth.

Correlations of plant variety preference among insect groups

There was no significant correlation between the number of honey bees and bumble bees per count per m^2 among the 32 varieties (r = 0.257, P = 0.155; Fig. 5.6a), suggesting that their preferences do not, generally, coincide. However, visitation by short-tongued bumble bees (*B. terrestris/lucorum* group) correlated significantly with visitation by long-tongued bumble bees (*B. hortorum* and *B. pascuorum* groups; r = 0.565, P < 0.001; Fig. 5.6b). We then looked at correlations in preference between both honey bees and bumble bees *vs.* other bee species, hover flies and butterflies and moths and found only

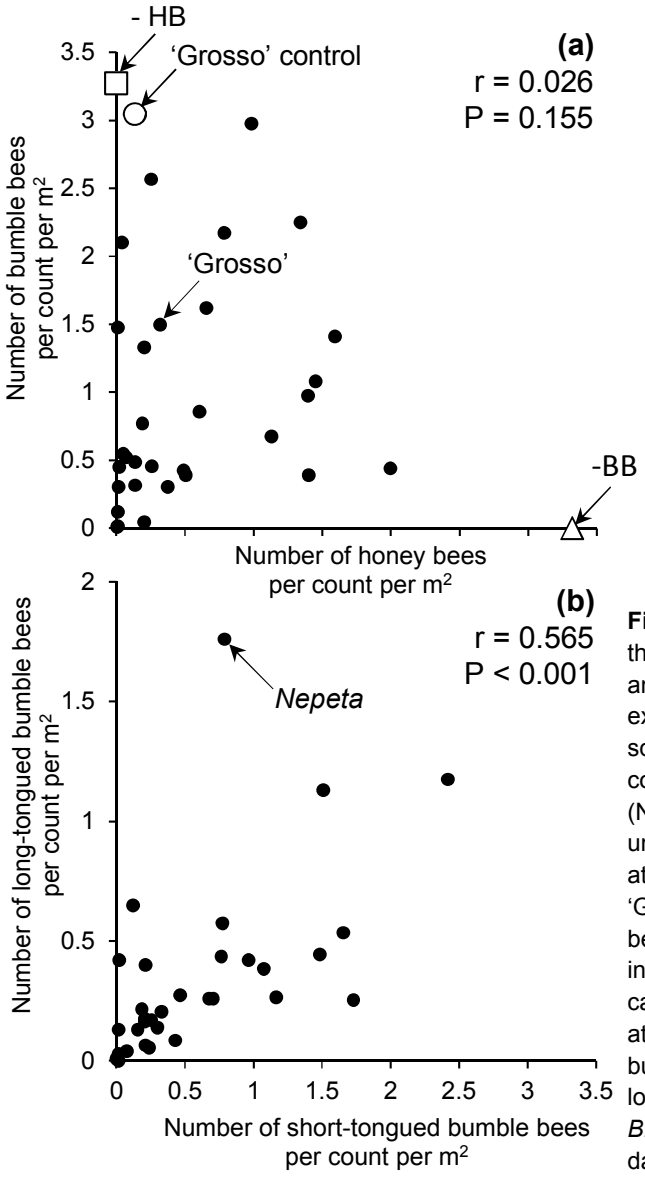


Figure 5.6. (a) The absence of correlation between the attractiveness of plant varieties to honey bees and bumble bees. Open symbols refer to three experimental treatments: honey bee exclusion (-HB, square), bumble bee exclusion (-BB, triangle) and control (circle) on *Lavandula* × *intermedia* 'Grosso' (N.J. Balfour, S. Gandy & F.L.W. Ratnieks, unpublished data). 'Grosso' control (open circle) attracted a higher number of bumble bees than 'Grosso' in our data (closed circle) due to the data being gathered on 4 days during the flowering peak in the former case, and over c. 3 months in the latter case. (b) Significant correlation between the attractiveness of plant varieties to short-tongued bumble bees (*Bombus terrestris/lucorum* group) and long-tongued bumble bees (*B. hortorum* and *B. pascuorum* groups). Black dots are means of two datasets (University of Sussex 2011 & 2012).

one of these correlations to be significant (bumble bees vs. butterflies & moths (r = 0.665s, P < 0.001); Fig. 5.7c). All other correlations were non-significant [honey bees *vs.* other bees (r = 0.169, P = 0.354), honey bees vs. hover flies (r = 0.251, P = 0.165), honey bees vs. butterflies & moths (r = 0.157, P = 0.390), bumble bees vs. other bees (r = -0.077, P = 0.675), bumble bees vs. hover flies (r = 0.266, P = 0.141)] (Fig. 5.7a–c). The significant correlations (Figs 5.6b and 5.7c) remained significant after Bonferroni correction (α = 0.05/8).

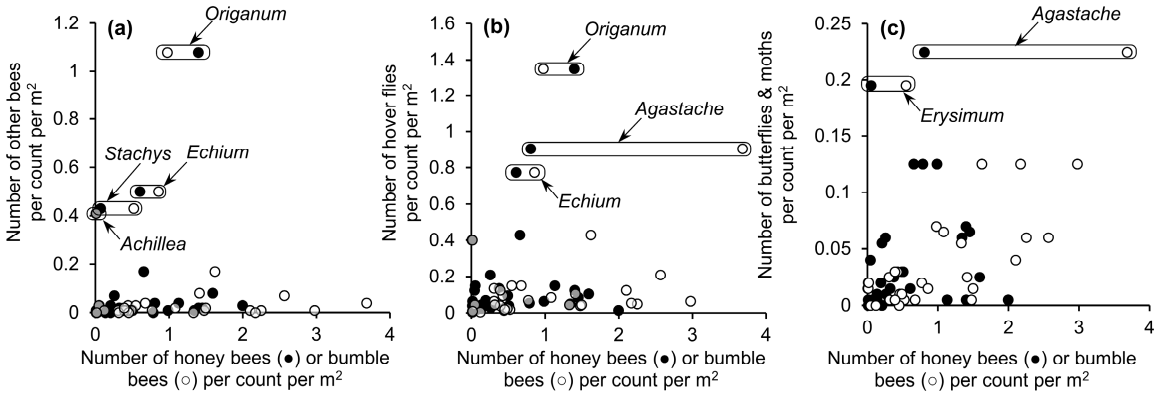


Figure 5.7. Correlations between the attractiveness of plant varieties to honey bees (●) & bumble bees (○) *vs.* other bees (a), hover flies (b), and butterflies & moths (c). The only significant correlation found was between bumble bees and butterflies & moths (r = 0.665, P < 0.001).

Discussion

The results showed very large, approximately 100-fold (c. 300-fold in 2011, c. 80-fold in 2012), variation among the 32 plant varieties at the University of Sussex in the total number of insects attracted. This clearly shows that there is great scope for making gardens and parks more bee- and insect-friendly by judicious plant selection. Importantly, this need not involve extra cost or gardening effort, or, indeed, a loss of aesthetic attractiveness, given that all the plants we compared were considered to be highly attractive, and were easily available at comparable and low prices. Our results can be considered as a contribution to the lists of recommended garden plants. However, this should be done with caution, as we only compared 32 varieties, which is a very small proportion of the thousands of varieties available (Cubey & Merrick, 2011) with similar habit (small shrubs and herbaceous plants suitable for a mixed border).

Attractiveness of plant varieties correlated strongly between 2011 and 2012 at the University of Sussex (Fig. 5.4a). It also correlated between the University of Sussex and the two additional flower beds at Plumpton College and Magham Down (Fig. 5.4b). This shows that our results apply generally to a wider area and are not unduly year- or location-specific. Some variation among locations may be due to local conditions (e.g. microclimate or soil type) or differences in the flower-visiting insect communities present. However, most insect species or groups we recorded are common in the UK and elsewhere, so would be present in many areas, but not necessarily in the same proportions. Similarly, some variation between the 2 years could be driven by annual fluctuations in insect populations. Additionally, in our study, the variation observed between years could be due to the different stages of establishment of perennial plant varieties. In 2011, the plants had been put into the patches soon after being delivered from suppliers, who grew them in pots, while in 2012, most varieties had had an extra year in the ground to establish.

Although variation in relative abundance of insects may explain a small proportion of variation in plant attractiveness, it cannot be a major factor, because the relative abundances of different taxa were broadly very similar among years and locations (Fig. 5.2). The majority of insects, at least 84% in each dataset, were bees, of which approximately one-third were honey bees, two-thirds were bumble bees plus a small percentage of other bee species. Hover flies were always the next most abundant taxon (7–10%). Butterflies and moths (1–3%) and all other insects (1–3%) were always a small percentage. Overall, our results suggest that garden plants can easily help bees, which showed up in large numbers, by providing forage. This agrees with Goulson *et al.* (2010), who found evidence of positive influence of urban gardens on bumble bee nest density and survival on a landscape scale. Bumble bees [maximum foraging range c. 1.5 km, (Osborne *et al.*, 2008b)] and especially honey bees [maximum foraging range c. 10-12 km, (Beekman & Ratnieks, 2000)] can forage at long distances from their nest and thus are able to exploit garden resources. By contrast, butterflies and moths, being relatively scarce garden flower-visitors, can perhaps not be as easily helped by garden flowers, despite not being central place foragers. There is also little evidence that the abundance of adult

resources, apart from shelter, has any impact on population size or trends in European butterflies (Thomas *et al.*, 2011).

The absence of a positive correlation between the attractiveness of plant varieties to honey bees and bumble bees (Fig. 5.6a) suggests that their foraging preferences do not, generally, coincide. Furthermore, the absence of a negative correlation seems to suggest that these bees do not appear to be in competition with each other. However, N.J. Balfour, S. Gandy & F.L.W. Ratnieks (unpublished data) showed competition on *L.* × *intermedia* 'Grosso' experimentally. In particular, honey bee numbers increased c. 30-fold on patches from which bumble bees were excluded (Fig. 5.6a). It is likely, therefore, that the lack of correlation between honey bees and bumble bees reflects both the effects of preferences and competition. As these two types of bees were the most abundant flower-visitors, each probably has the capacity to affect the other via consumptive competition (N.J. Balfour, S. Gandy & F.L.W. Ratnieks, unpublished data). In the case of *L.* × *intermedia* 'Grosso', the mean corolla tube length of 7.2 mm was experimentally shown to disadvantage honey bees (mean tongue length 6.6 mm) vs. bumble bees (mean tongue length 7.8 mm) by causing longer flower-handling times (Balfour *et al.*, 2013).

Plant variety attractiveness was similar between the short-tongued (*B. terrestris/lucorum* group) and the long-tongued (*B. hortorum* and *B. pascuorum* groups) bumble bees, perhaps, reflecting preferences common to *Bombus* in general (Fig. 5.6b) or the fact that tongue length variation among bumble bees had little effect in our gardens, despite reported effects being noted in the literature (Goulson *et al.*, 2005; Goulson *et al.*, 2008a). *Nepeta* × *faassenii* 'Six Hills Giant' stood out from this correlation, being very attractive to long-tongued bumble bees [length 8.5–12.5 mm (Goulson *et al.*, 2005)], but relatively unattractive to short-tongued species (length 7.5–7.6 mm), possibly due to its relatively long corolla tube (11.9 ± 0.2 mm). However, other plant species with similarly long corolla tubes were attractive to short-tongued species due to large corolla width (e.g. *E. vulgare*), which allowed short-tongued insects to place their whole head or body far into the flower, reducing or eliminating the need for a long tongue. In general, attractiveness did not correlate between honey bees and bumble bees on the one hand,

and other bees, hover flies and butterflies + moths on the other, with the exception of the positive correlation between bumble bees *vs.* butterflies + moths (Fig. 5.7). However, certain plants stood out as particularly good for other, non-*Apis* and non-*Bombus*, bees (*Origanum vulgare*, *E. vulgare*, *S. byzantina*, *Achillea millefolium*), hover flies (*O. vulgare*, *A. foeniculum*, *E. vulgare*) and butterflies & moths (*A. foeniculum*, *Erysimum linifolium*). Interestingly, three of the four species particularly attractive to other bees are also native to Britain, suggesting that native plants may be more important for non-*Apis* and non-*Bombus* bees.

The factors potentially responsible for variation in attractiveness among plant varieties are diverse (e.g. size, shape, colour or scent, reviewed by Pellmyr (2002)). However, as the insects counted were flower-visiting foragers, this variation is presumably largely a result of foraging choices based on nectar and pollen rewards in bees (Seeley, 1995; Goulson & Osborne, 2010) and hover flies (Haslett, 1989) and nectar rewards in other insects (Kim *et al.*, 2011). Our data showed no effect of corolla tube length (Appendix 5.3). However, in specific cases, corolla tube length may be important. In the case of lamb's ear (*Stachys byzantina*), its attractiveness to wool-carder bees (*Anthidium manicatum*) is probably due to the abundant leaf trichomes (pubescence) and possibly trichome secretions, which are collected by females as nest lining material (Müller *et al.*, 1996; Payne *et al.*, 2011). In addition, lamb's ear flowers are also visited by wool carders. Some plants may be more attractive than others by virtue of their longer flowering period. For example, *N.* × *faassenii* 'Six Hills Giant' and *Erysimum linifolium* 'Bowles Mauve', which are sterile hybrids unable to set seed, had flowering periods extending far beyond our c. 3-month observation periods. Indeed, *E. linifolium* flowers for approximately 9 months per year in Sussex. The attractiveness of such varieties is, therefore, underestimated in our data.

Closer examination of lavenders showed that hybrid *L.* × *intermedia* varieties were more attractive than both *L. angustifolia* varieties and *L. stoechas* (Fig. 5.5). This difference was not explained by either bloom duration or corolla tube length. In addition, flower colour, which ranged from light (e.g. white 'Arctic Snow', 'Edelweiss', rose 'Rosea') to

more typical shades of blue, did not appear to be an important factor (Fig. 5.5). We note that *L.* × *intermedia* varieties tended to be larger plants with taller inflorescences than *L. angustifolia* or *L. stoechas*. However, the definitive explanation causing the difference in attractiveness remains unknown and would be a valuable subject for further research.

Within the *Dahlia* genus, the two open-flowered varieties ('Bishop of Llandaff' and 'Bishop of Oxford') were consistently more attractive compared with the two varieties with highly modified flower forms (pompon 'Franz Kafka', semi-cactus 'Tahiti Sunrise'). This was likely due to the limited accessibility of disc florets, which provide nectar and pollen, due to the unusual shapes of the ray florets resulting from plant breeding. Additionally, the increased size and number of ray florets may be accompanied by a reduction in the number of disc florets, as compared to the open-flowered varieties. These results are supported by data from a survey of garden plants in a public garden in the nearby town of Lewes, where 'open' flowered varieties attracted significantly more insects than 'closed' flowered varieties (Chapter 6).

Among other notable results is the pattern seen on *B. officinalis*, where the vast majority of its visitors were honey bees (mean 81.3% per dataset). The highest proportions of butterflies and moths were recorded on *E. linifolium* (mean 11.1% per dataset). *Pelargonium* × *hortorum* 'Cramden Red' was consistently the least attractive variety in each dataset, with only 0.027 mean insects per count per m^2 recorded. The four native species and the four wildtype varieties (Fig. 5.3; Appendix 5.1) were not consistently more or less attractive than exotic or horticulturally modified varieties, showing that nativeness *per se* is not an important factor, and that horticultural modification need not reduce flower attractiveness to insect flower-visitors. Indeed, the case of lavender shows that the breeding of hybrid varieties can make plants more attractive to insects. In addition, varieties with very long bloom durations, such as *E. linifolium* 'Bowles Mauve' and *N.* × *faassenii* 'Six Hills Giant', were sterile hybrids. As the plant hormones associated with seed and fruit development may inhibit flowering [e.g. gibberellins in woody angiosperms (Pharis & King, 1985; Anthony, 2006; Davies, 2010)], sterility is an obvious way in which

a garden plant can be simultaneously made more attractive to humans and flower-visiting insects. Sterility may also reduce the risk of invasiveness.

Our study used deliberately planted patches of 1 × 1 m. However, patch size does not affect the number of insects per unit area that visit garden plants in a range of patch areas from 0.1 to 3.1 m^2 (Chapter 4). Thus, studies to quantify flower attractiveness to insects can use existing patches in less standardized settings, such as gardens and parks, where patch size is measured and rates are calculated per unit area. The insect groups, including the bumble bee subgroups (Fussell & Corbet, 1992), used in this study are simple enough to be differentiated by the public with little training, as was demonstrated by us in a series of workshops in 2011, 2012 and 2013 using the experimental flower bed at the University of Sussex. These methods could form the basis of large-scale 'citizen science' projects involving the help of many volunteers in gathering the data (Dickinson *et al.*, 2012; Tweddle *et al.*, 2012), or smaller projects run by interest groups, such as gardening or beekeeping clubs, or even schools or colleges.

Chapter 6

Survey of insect visitation of ornamental flowers in Southover Grange garden, Lewes, UK

Mihail Garbuzov, Elizabeth E. W. Samuelson, Francis L. W. Ratnieks

Abstract

Ornamental flowers commonly grown in urban gardens and parks can be of value to flower-visiting insects. However, there is huge variation in the number of insects attracted among plant varieties. In this study, we quantified the insect attractiveness of 79 varieties in full bloom being grown in a public urban garden that is popular due to its beautiful flowers and other attractions. The results showed very clearly that most varieties (77%, n = 61) were either poorly attractive or completely unattractive to insect flower visitors. Several varieties (19%, n = 15) were moderately attractive, but very few (4%, n = 3) were highly attractive. Closer examination of *Dahlia* varieties showed that "open" flowered forms were approximately 20 times more attractive than "closed" flowered forms. These results strongly suggest that there is a great potential for making urban parks and gardens considerably more bee- and insect-friendly by selecting appropriate varieties.

Introduction

Urban gardens and parks are increasingly recognized as of value to wildlife (Goddard *et al.*, 2010; Owen, 2010; Hennig & Ghazoul, 2012). Many garden plants are introduced from other parts of the world (Kendal *et al.*, 2012), and may present different value to native wildlife. For example, butterfly larvae typically have a narrow range of suitable food plants (Dyer *et al.*, 2007). Plants grown outside their original geographic distribution often support fewer herbivores than closely related native species (Perre *et al.*, 2011). However, introduced plants also have generic value to wildlife, such as a bird that can nest in an

introduced tree as easily as in a native one. The flowers of introduced plants can be of value to flower-visiting insects. Flowers are generically attractive due to their shape, colour and especially their nectar and pollen rewards. Nectar is predominantly a solution of various sugars, mostly sucrose, glucose and fructose, and is an energy source for many insects (Nicolson & Thornburg, 2007). It is common to see native insects foraging on flowers of introduced plants. For example, British butterflies take nectar from *Buddleja davidii*, commonly known as the butterfly bush, which is a plant native to China that is now commonly grown in British gardens (Tallent-Halsell & Watt, 2009), although none use it as a larval food plant (Eeles *et al.*, 2012). However, *B. davidii* is used as a larval food plant by a few highly polyphagous British moths (Owen, 2010).

Many ornamental plants grown in urban gardens and parks are attractive to flower-visiting insects (Comba *et al.*, 1999a,b; Pawelek *et al.*, 2009). Recent research shows that ornamental garden flowers that are readily available for purchase in the UK at similar prices vary greatly, approximately 100-fold, in their attractiveness to foraging insects such as bees, hover flies, and butterflies (Chapter 5: Garbuzov & Ratnieks, 2014a). Thus, there is a great "no cost" potential for gardeners and park managers to help flower-visiting insects by planting varieties attractive to insects. Many gardeners are potentially interested in helping wildlife in their gardens. A survey of UK gardeners showed that 31% deliberately choose plants attractive to wildlife (Mew *et al.*, 2003), and the interest and enthusiasm of gardeners appear to be on an increase. Many garden centres now promote certain plant varieties as bee- or butterfly-friendly and the UK's Royal Horticultural Society (RHS) has even started an initiative by labelling some varieties with the "Perfect for Pollinators" trademark logo [www.rhs.org.uk]. However, the basis on which these recommendations are made is not clear.

The aim of this study was to estimate how useful to insects the plants currently grown in gardens are. We did this by surveying ornamental garden flowers in a local garden which is popular and known for the beauty of its flower displays. We determined the area of each variety and quantified flower visitation by all foraging insects, which were mainly bees and flies. In total there were 79 varieties in full bloom at the time of the survey.

Interestingly, our results showed that only 4% were highly attractive, while 30% were not visited by a single insect, and another 47% visited by very few. Our study suggests that gardens have great room for improvement in providing nectar and pollen for bees and other insects.

Methods

Study location

The study was carried out in Southover Grange garden, which is located near the centre of the town of Lewes (area 11 km^2, population 16,000) in the county of East Sussex, UK. The area surrounding the garden had mostly private residential houses and, due to the small size of the town, was relatively close to agricultural land (<1 km). Southover Grange house and garden is a heritage site of historical significance open to the public and managed by the Lewes District Council (n. d.). It has an area of approximately 1.5 ha and is managed for non-sport recreation, with lawns, ornamental trees and shrubs, annual, and perennial herbaceous flower beds (Fig. 6.1). No pesticides are used in the garden to control herbivorous insects. The place, with its beautiful surroundings, is a great attraction to local residents, as well as visitors and tourists.

Figure 6.1. Part of Southover Grange garden in Lewes, East Sussex, UK during the late summer blooming period, August 2012.

Data collection

The flower beds in Southover Grange garden are managed in such a way as to produce two main blooming periods per year, one in spring and another in late summer. Our survey was conducted over 2 days within the late summer blooming period, when most plant varieties were at or near their flowering peak. Indeed, varieties flowering in late summer have the potential to be more useful to bees and other insects than varieties flowering in spring, as late summer is the time of year when honey bee foraging distances in this part of Sussex (Couvillon *et al.*, 2014a), and probably much of Britain (Beekman & Ratnieks, 2000), are greatest, indicating low overall forage availability. We surveyed only those varieties (n = 79) that were at or near full bloom during the data collection period.

We made repeated counts of flower-visiting insects on each patch containing a single variety. These counts were near-instantaneous 'snapshots' (<10 sec), in which the observer recorded the number of foraging insects at an instant of approaching a patch by scanning it by eye (Chapter 5: Garbuzov & Ratnieks, 2014a). In total, we took 15 counts from each patch (n = 117 patches, some varieties were grown in more than one patch) over 2 days (21 and 23 August 2012). The weather conditions on survey days were very good for insects: sunny, calm and warm (peak temperature 21–22 °C).

The insects were identified and grouped to taxa as follows: (i) honey bees (*Apis mellifera*), (ii) 2-banded white-tailed bumble bees (*Bombus terrestris/lucorum* group, after Fussell & Corbet, 1992), (iii) banded red tailed bumble bees (*Bombus pratorum* group), (iv) brown bumble bees (*Bombus pascuorum* group), (v) other bumble bees, (vi) other bees (non-*Apis* and non-*Bombus*), (vii) hover flies (Diptera: Syrphidae), (viii) other flies (non-Syrphidae), (ix) butterflies & moths (Lepidoptera), and (x) all other insects. Since the number of insects foraging on a patch per unit area is not affected by patch area (Chapter 4), it is possible to make unbiased comparisons of plant varieties grown in patches of different size. The attractiveness of each variety was, therefore, expressed as the total number of insects per count per square meter. The area of each variety in each patch was measured by approximating it to the nearest geometric shape, for example, a square,

a rectangle, a circle, or a combination thereof. Where there were several patches per variety the data were combined (total areas of each variety are listed in Appendix 6.1).

The list of plant varieties surveyed with some of their characteristics is provided in Appendix 6.1. The plant varieties were identified with the help of information provided by Richard Eborn of the Lewes District Council. A few varieties could not be fully identified.

Results

Insect flower visitors

In total, 2235 insects were recorded. The relative and absolute abundance of taxonomic groups are shown in Fig. 6.2. Flower visitors were predominantly bees (74.8%) and flies (24.3%) of which 35.5% were honey bees, 37.7% bumble bees, 1.6% other bee species, 20.4% hover flies, and 3.8% other fly species. Butterflies and moths were 0.7% and other insects 0.3%.

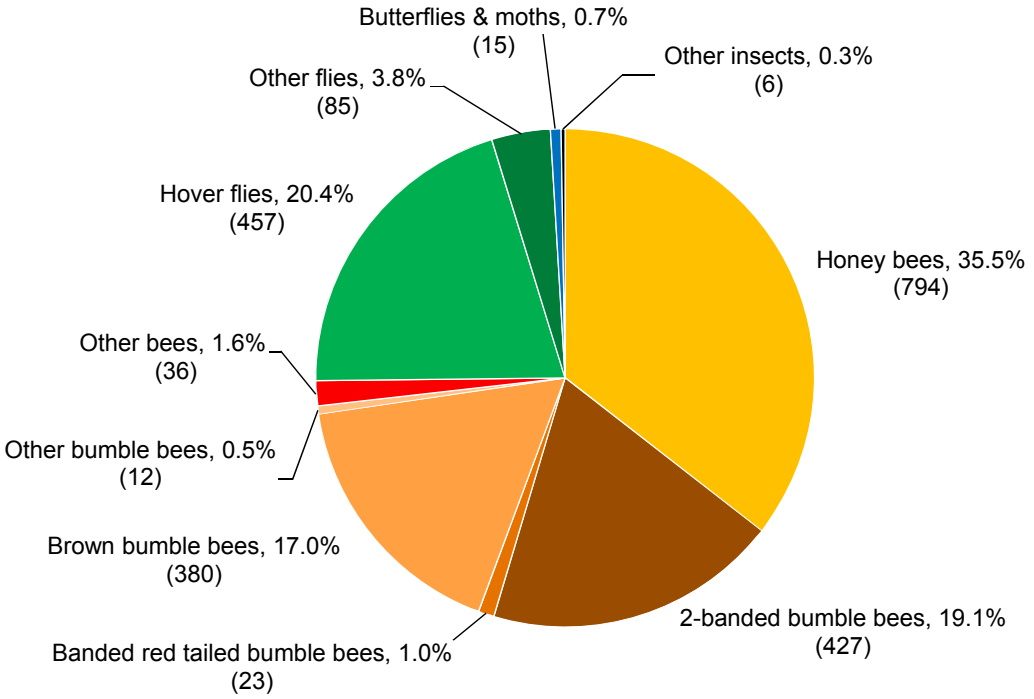


Figure 6.2. Relative and absolute numbers of insects in the 10 groups.

Attractiveness of plant varieties to insect flower visitors

Plant varieties varied enormously in their attractiveness to insect flower visitors, approximately 1000-fold from the most attractive to the least attractive that had non-zero insects. Furthermore, the frequency distribution of attractiveness was highly skewed to the right, revealing that most plant varieties were unattractive to insects (Fig. 6.3). Thirty percent (n = 24) of varieties were completely unattractive (0 insects recorded), with a further 47% (n = 37) attracting very low numbers (0.01–1/count m^2). Nineteen percent (n = 15) were moderately attractive (1–5/count m^2). Very few, 4% (n = 3), were highly attractive (>10 /count m^2).

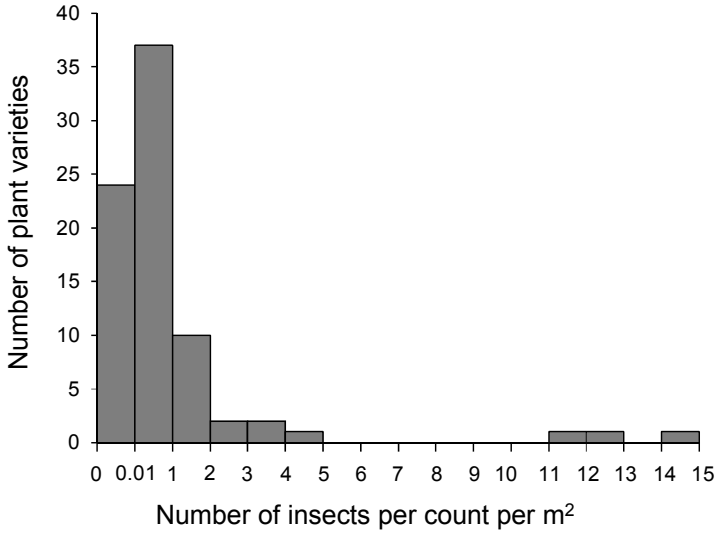


Figure 6.3. Frequency distribution of insect-attractiveness of the 79 plant varieties surveyed. Note the first bin (0–0.01) is not to scale with others and includes only those varieties that attracted exactly zero insects.

Comparison of Dahlia varieties

One of the flower beds in Southover Grange garden was composed exclusively of 11 *Dahlia* varieties. We have, therefore, examined the dahlia results in more detail, and in particular, compared "open" flowered varieties (e.g., single or semi-double) with "closed" flowered varieties (e.g., fully double, decorative, pompon or cactus). GLM confirmed that not all varieties were equally attractive to insects ($F_{10,154} = 24.18$, $P < 0.001$). In addition, flower form (open vs. closed) was a significant factor ($F_{1,163} = 85.23$, $P < 0.001$) that explained 34% of variation ($R^2 = 0.339$), with "open" varieties (mean ± SE = 0.97 ± 0.13

insects/count m^2) approximately 20 times more attractive than "closed" varieties (mean ± SE = 0.05 ± 0.13 insects/count m^2). Of the four "open" varieties, two were attractive to insects and two somewhat attractive (Fig. 6.4). In contrast, of the seven "closed" varieties, only two were somewhat attractive, while five were unattractive.

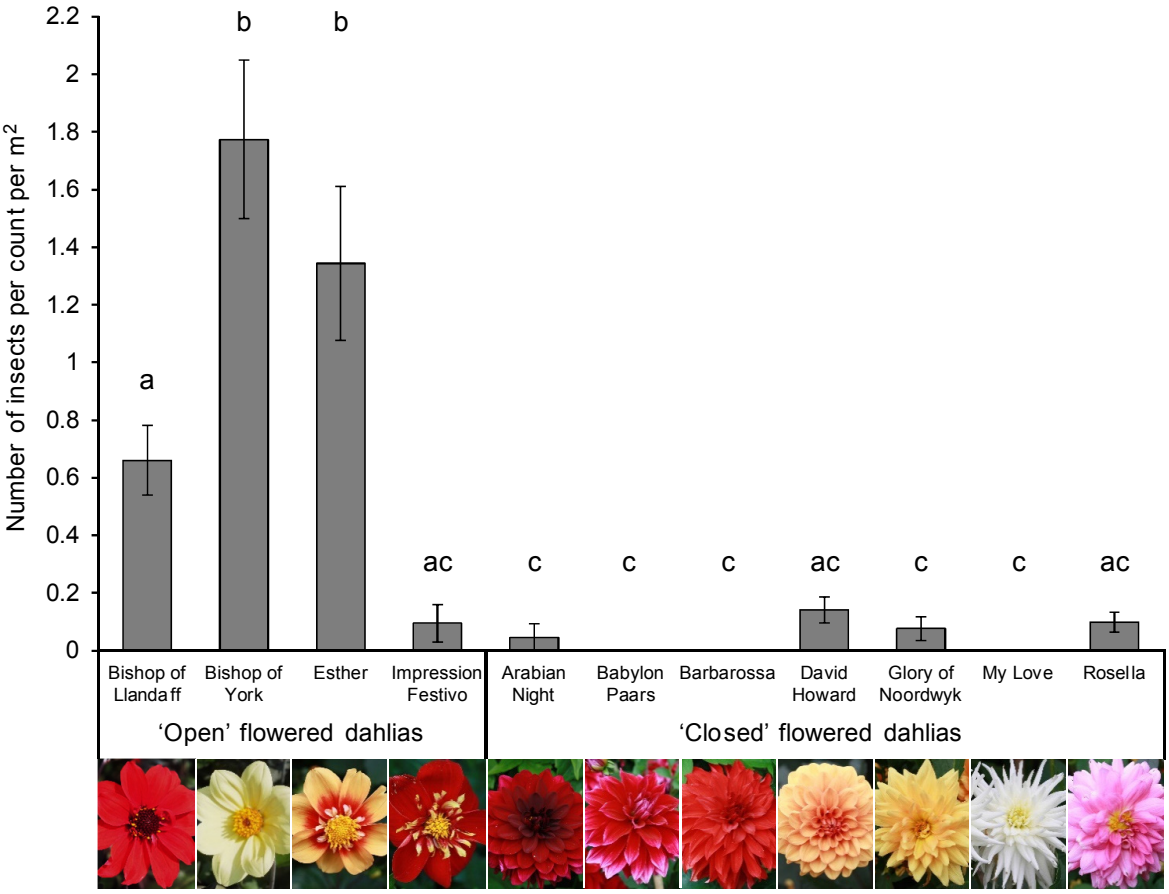


Figure 6.4. Mean ± standard error numbers of insects per count per m^2 recorded on 11 *Dahlia* varieties. Letters above bars denote significance of Tukey's *post-hoc* pairwise comparison test at α = 0.05.

Discussion

Our results clearly show that most flower varieties being grown in Southover Grange garden were not attractive to insects. Although the overall pattern observed is robust, specific results pertaining to particular varieties should be interpreted with caution, as varieties may be subject to idiosyncratic effects, such as those of patch location with respect to neighbouring patches or other factors, or the timing of nectar production. It will also require additional surveys to determine if this is a general pattern in parks and gardens in the UK and elsewhere. However, given that Southover Grange garden used

many widely available and commonly grown plants to provide colour, and that colour is a goal of many gardeners, we predict that many other gardens will also have low proportions of insect-friendly flowers.

The comparison of the *Dahlia* varieties is interesting as it shows that the breeding of garden flowers to have unusual morphology, such as in the cactus or pompon dahlias, can reduce their value to insects. The open varieties, even those such as 'Bishop of Llandaff', which is semi-double (i.e. with an increased number of "petals", actually ray florets in each composite flower or inflorescence), have easily accessible disc florets that provide nectar and pollen (Fig. 6.5b). Fig. 6.5c shows two composite flowers of the most attractive of the closed varieties, David Howard. Only at the end of the blooming period are the disc florets accessible, and their amount is considerably less than in the open varieties shown for comparison, 'Bishop of York' and 'Bishop of Llandaff' (Fig. 6.5a,b).

Figure 6.5. *Dahlia* flower varieties: (a) 'Bishop of York', single, (b) 'Bishop of Llandaff', semi-double, (c) David Howard, fully double decorative. In David Howard, disc florets providing nectar and pollen are obscured by the ray florets in the newly opened flowers (c, left) and become accessible only towards the end of the flower's life (c, right). In addition, the amount of disc florets in (c) is lower than in (a).

These results strongly suggest that there is a great potential to make urban parks and gardens considerably more bee- and insect-friendly by appropriate plant selection. Southover Grange garden is beautiful, and the varieties chosen lead to a spectacular display of many colours. But with many thousands of garden flower varieties available (e.g. over 70 000 in the RHS Plant Finder alone, Cubey & Merrick, 2011) we are certain that having insect friendly plants need not lead to a reduction in overall attractiveness.

Selecting insect-friendly plant varieties requires information on insect-attractiveness. Some of this information may be available in the numerous recommended plant lists, produced by both amateurs (e.g. Creeser, 2004; Lavelle & Lavelle, 2007) and professional organizations (e.g. IBRA, 2008; RHS, 2011; Xerces Society, 2011; Kirk &

Howes, 2012). These recommendations appear to be based mainly on personal observations and opinions, rather than empirical data. However, the best plants from this survey (*Sedum* and *Origanum*) tend to be often recommended in lists, being featured in 14 of 15 lists in one sample (Chapter 3), implying that well-informed opinion, perhaps backed by extensive observation, can be nearly as good as rigorously collected empirical data.

Our study presents a short survey with useful, but necessarily limited results. Furthermore, the methodology used in our survey could be used to assess the insect attractiveness of flower patches that are already being grown, by gardeners themselves or by the general public as "citizen science". Such surveys require relatively little effort. For example, our survey took three days of fieldwork, of which two were spent counting insects and one was used to measure flower patch areas. In addition, the methods, including insect identification, are simple to learn. Alternatively, given more time and resources, more detailed and standardized trials could be performed, which would provide a more accurate and complete picture (e.g. Chapter 5: Garbuzov & Ratnieks, 2014a).

Chapter 7

Using the UK national collection of asters to compare the attractiveness of 228 varieties to flower-visiting insects

Mihail Garbuzov, Francis L. W. Ratnieks

Abstract

Wildlife-friendly gardening practices can help conserve biodiversity in urban areas. These include growing ornamental plant varieties attractive to flower-visiting insects. However, varieties vary greatly in attractiveness. Therefore, there is a need to quantify the attractiveness of different varieties in order to give objective advice to gardeners. Here, we used the UK's national collection of asters at the Picton Garden to compare the numbers of flower-visiting insects. We counted and identified flower-visiting insects on 228 aster varieties growing in discrete patches that flowered during the survey period, 14 September – 20 October 2012. Thirty counts were made from each patch. In each variety, we also determined overall capitulum size and that of the central disc floret area, ray floret colour (blue, red, purple or white), and scored attributes relevant to gardening: attractiveness to humans, ease of cultivation, UK availability. There was great variation among varieties in the numbers of insects counted on flowers, ranging from 0.0 to 15.2 per count per m^2, and highly skewed, with most being unattractive. The same pattern held for the two main insect categories, honey bees and hover flies, which comprised 28% and 64% of all insects, 92% in total. None of the floral traits correlated significantly with attractiveness to insects. There were also no correlations of attractiveness to insects with gardening attributes. Our study shows the practicality of using a national collection for quantifying and comparing the attractiveness of ornamental varieties to flower-visiting insects. It would have been prohibitively expensive and time consuming to grow these in an experimental garden specifically to measure attractiveness. The results showed that choosing varieties carefully

will be of significant benefit to flower-visiting insects, given that most attracted few or zero insects. The results also show that growing insect-attractive aster varieties is a no-cost option in terms of beauty and workload.

Introduction

Wildlife is facing increasing pressure from human activity (Barnosky *et al.*, 2011). These pressures can potentially be offset, at least to an extent, by various practices including agri-environment schemes (Batary *et al.*, 2011) and wildlife-friendly gardening practices in urban and suburban parks and gardens (Good, 2000; Shwartz *et al.*, 2013). Flower-visiting insects such as bees and hover flies can collect pollen and nectar from many ornamental garden plant varieties (Comba *et al.*, 1999b; Frankie *et al.*, 2005; Matteson *et al.*, 2008; Hanley *et al.*, 2014). However, ornamental plants are extremely variable in their attractiveness to flower-visiting insects, ranging 100-fold or more from highly attractive to almost never visited (Chapter 5: Garbuzov & Ratnieks, 2014a; Chapter 6). For example, counts of foraging insects showed that, in the same garden, flowers of *Pelargonium* × *hortorum* 'Cramden Red' were being visited by only 0.02-0.09 insects per m^2 per count versus 5.26-5.95 for *Agastache foeniculum* 'Blue Fortune' and 2.75-7.17 for *Origanum vulgare* 'Hirtum' (Chapter 5: Garbuzov & Ratnieks, 2014a).

The public has a great interest in helping wildlife by planting bee and insect-friendly garden flowers, and many lists of recommended plants have been produced (Chapter 3). The authors of these include well-respected national and international organizations, such as the UK's Royal Horticultural Society (RHS, 2011), International Bee Research Association (IBRA, 2008; Kirk & Howes, 2012) or North America's Xerces Society for Invertebrate Conservation (Xerces Society, 2011), as well as government organizations (e.g. Natural England, 2007) and individuals (e.g. Creeser, 2004). However, most of the recommendations in these lists appear to be based mainly on opinion, although often backed by personal experiences and observations (Chapter 3).

How can we determine more objectively which ornamental plants are most attractive to flower-visiting insects? In principle this is simple. All that is needed is to count insects on flowers and compare the numbers and types attracted per unit area. But in practice this is not so simple. Our earlier research compared 32 varieties in a specially-planted garden of summer-flowering varieties, each replicated in two 1×1 m beds (Chapter 5: Garbuzov & Ratnieks, 2014a). But there are tens of thousands of varieties available (Cubey & Merrick, 2011), which is clearly beyond what can be compared in an experimental garden. Another approach is to compare attractiveness using existing gardens and parks (Frankie *et al.*, 2005; Pawelek *et al.*, 2009). In this way we compared 79 summer-flowering varieties in an urban park managed by a local town council (Chapter 6).

A further approach, which we used in this study, is to take advantage of existing plant collections. In the UK there are hundreds of collections of particular plant groups accredited under the National Collection scheme and regulated by Plant Heritage, the organization formerly known as the National Council for the Conservation of Plants & Gardens (NCCPG). The aim of these collections is "to document, develop and preserve a comprehensive collection of one group of plants in trust for the future" (www.nccpg.com). Collections also provide an opportunity for gardeners and growers to observe and compare a range of characteristics of interest among many varieties, including appearance, size, attractiveness to humans etc. Similar collections occur in other countries, such as the North American Plant Collections Consortium (NAPCC) in the United States (www.publicgardens.org/napcc) and the Network Plant Collections in Germany (Netzwerk Pflanzensammlungen, www.netzwerkpflanzensammlungen.de). Here, using the UK's national collection of asters, we compared the attractiveness of 228 varieties to flower-visiting insects.

Methods

Study location

The study was carried out at the national collection of asters in the Picton Garden and The Old Court Nurseries, Colwall, Herefordshire, UK. The collection comprises several hundred varieties on display and is part of the Picton family's business specializing in growing, breeding and selling asters (www.autumnasters.co.uk).

What is an aster?

Asters are known under many colloquial names, such as Michaelmas daisies in Britain or fall roses in the United States. These names used to refer specifically to the genus *Aster* (Picton, 1999). However, due to advancing systematic knowledge, many former species of Aster were re-classified into other genera, chiefly *Symphyotrichum*, within the North American clade of the tribe Astereae (Brouillet *et al.*, 2009). This nomenclature has been widely adopted in the United States, including in the Flora of North America (http://floranorthamerica.org), but not yet in Britain or Europe (e.g. Botanical Society of Britain & Ireland, www.bsbi.org.uk). Throughout this chapter, aster species and varieties will be treated as members of the genus *Aster*, i.e. *Aster sensu lato* (Nesom, 1994), as in much of the older literature.

Why study asters?

We chose asters as they are a large and popular group of perennial ornamental herbaceous flowers that are widely grown in the UK and many other countries. Different varieties, or cultivars, vary considerably in appearance with a range of sizes, colours, flowering phenologies and other traits. Most ornamental varieties are derived from several species

native to North America, chiefly the New York aster (*Aster novi-belgii*) and the New England aster (*Aster novae-angliae*), but some are also derived from popular hybrids, such as the Frikart's aster (*Aster* × *frikartii*), a hybrid of the European *Aster amellus* and the Himalayan *Aster thomsonii* (Picton, 1999). Asters can have an important place in gardens, as they are among the last flowers to bloom in the year and so provide autumn colour in various shades of blue, red, purple and white. Flowering phenology varies slightly across species and varieties, but, in general, begins in early to mid-September and finishes in mid to late-October. Although autumn foraging conditions in England are not as challenging as they are in summer, as indicated by the distances encoded in honey bee waggle dances (Couvillon *et al.*, 2014a), they are not as good as in spring. Thus, autumn may be an important time to provide additional sources of pollen and nectar for flower-visiting insects, as there is a general scarcity of flowers other than ivy, *Hedera helix* and *Hedera hibernica*, (Chapter 8: Garbuzov & Ratnieks, 2014b).

Plant and patch characteristics

We included in our study only those varieties growing in discrete patches, which was the majority of the collection (total n = 246 varieties in 299 patches). The collection was surveyed in 2012 on three visits, whose dates were chosen to correspond approximately to the early (14-15 September), middle (28-29 September) and late (19-20 October) flowering periods of most varieties (Fig. 7.1). On each visit, the bloom intensity of each patch was quantified by assigning it a score on a four-point scale (0, absence of bloom; 1, <⅓ of maximum; 2, ⅓–⅔ of maximum; 3, full bloom, >⅔ of maximum; after Anderson and Hubricht (1940)). A few varieties that did not start blooming before the end of surveying (n = 15) or had finished blooming before the start (n = 3) were excluded, leaving 228 varieties in the dataset. Patch areas were measured by approximation to the nearest simple geometric shape (usually a rectangle, e.g. Fig. 7.2b), and ranged from 0.1 to 5.6 m^2 (mean±SD = 0.6±0.5 m^2).

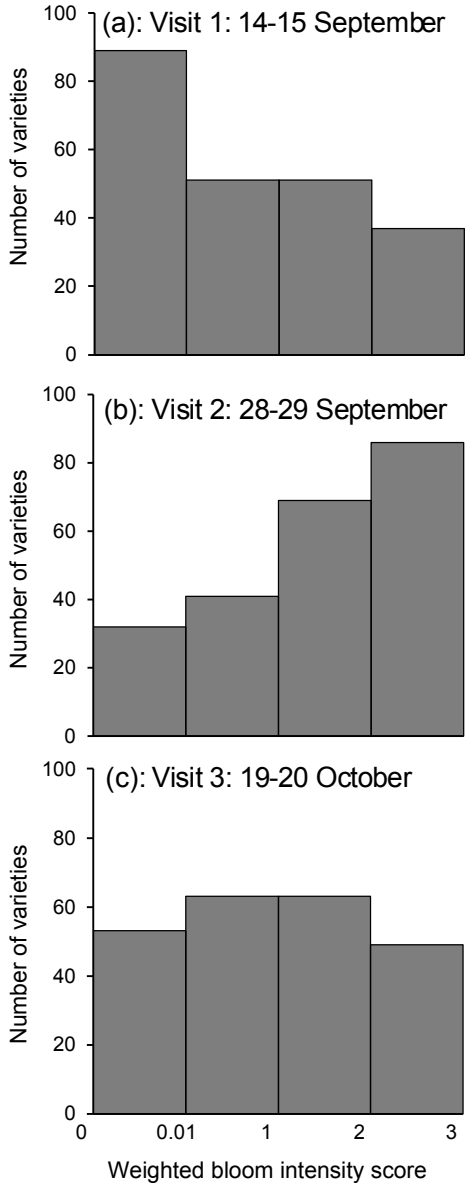


Figure 7.1. Frequency distributions of weighted bloom intensity scores of 228 *Aster* varieties at three visits to the national collection during the autumn of 2012: (a) 14-15 September, (b) 28-29 September, (c) 19-20 October. Bloom intensity scores for varieties blooming asynchronously in more than one patch were weighted by patch area.

Ray floret colour was assigned into one of the following categories: (i) red (including pinks, crimsons and burgundies), (ii) blue (including light and dark blues), (iii) purple (including lilac) and (iv) white. Floral size measures, disc floret area and total capitulum area, were measured from digital photographs of one representative capitulum per variety, with a ruler held in its flat plane (Fig. 7.2c), using the software ImageJ v. 1.45s (National Institute of Health, Bethesda, MD, USA). A flower head of typical size was chosen. Size varied little within varieties, but considerably among varieties. (M.G., pers. obs., see also Fig 7.2b,e).

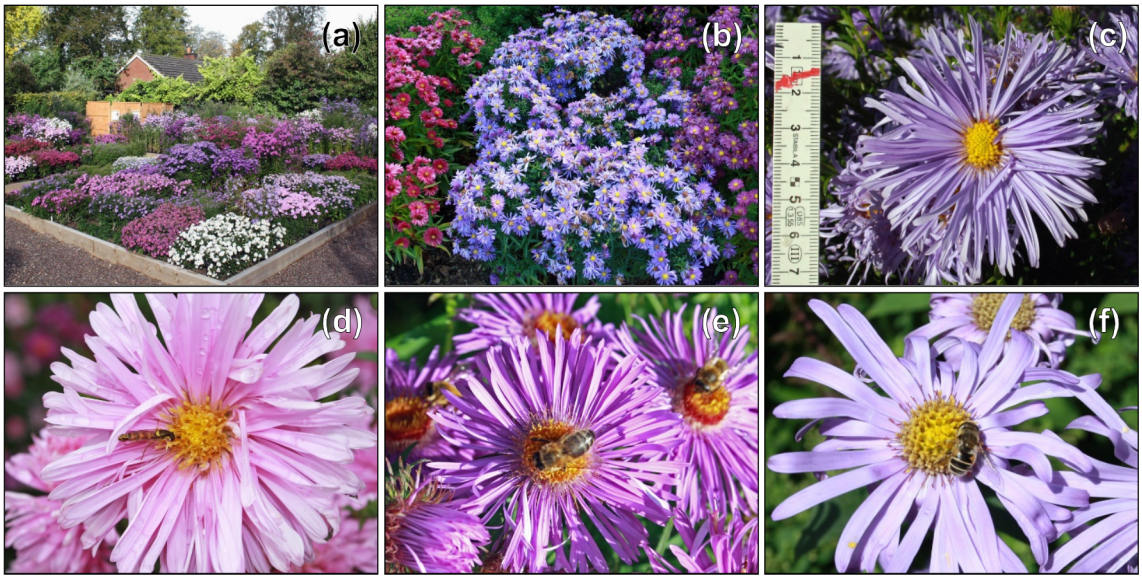


Figure 7.2. Asters in the Picton Garden. (a) Large square beds of *Aster novi-belgii*. (b) Patch of *A. novi-belgii* 'Blue Lagoon' of approximately rectangular shape next to *A. novi-belgii* 'Jenny' (left, red) and *A. novi-belgii* 'Elsie Dale' (right, purple). (c) Capitulum of *A. novi-belgii* 'Blue Radiance' photographed with a ruler in its flat plane for size measurement. Flowers of (d) *A. novi-belgii* 'Coombe Margaret', (e) *Aster novae-angliae* 'Augusta' and (f) *Aster amellus* 'Gründer' being visited by honey bees (e) and hover flies (d, f).

Quantifying insect visitation

On each visit to the collection, the insects visiting flowers on each patch were counted and identified 10 times over 2 days (= 30 times across the three visits). Each count took <10s, with c. 1 hour or more between counts. This interval between successive counts at the same patch minimized the chance of recording the same individual insect on the same foraging trip or bout. When being counted, the insects were also identified into the following groups: (i) honey bees, *Apis mellifera*, (ii) bumble bees (*Bombus* spp.), (iii) hover flies (Diptera: Syrphidae), (iv) other flies (non-syrphid Diptera), (v) butterflies (Lepidoptera) and (vi) all other insects.

Variety attributes relevant to gardening

Attributes relevant to gardening were also quantified. Attractiveness from the human perspective was scored on a three-category scale as 'low', 'medium' and 'high'. Ease of cultivation was also scored into three categories as 'easy' (requiring no special care or

skills), 'intermediate' (requiring some special care or skills), and 'specialist' (requiring extensive gardening experience to grow). Availability in the UK was scored into four categories: 'very rare' (unlikely to be available for sale outside the national collection), 'rare', 'common', and 'very common' (widely available throughout the country). Although these measures involve a degree of subjectivity, they were scored by Helen Picton, one of the owners of the national collection, who has extensive knowledge and experience in the sale, breeding and cultivation of asters.

Statistical analyses

All statistical analyses were performed in R v. 3.0.2 (R Core Team, 2013). For varieties that were grown in more than one patch, both counts and patch areas were summed. Due to the fact that plants of the same variety grown in different patches sometimes bloomed asynchronously, we calculated mean bloom intensity scores for each variety weighted by patch area. The dataset was then collapsed across the 'variety' by averaging all other variables. For example, in the case of insect visitation, these were means of the 30 counts recorded during the whole study period. Additionally, as previous research has shown a linear relationship between the insect count and patch area in garden-scale flower patches (Chapter 4), the insect counts were divided by patch area to form the response variables in the analyses.

Due to low numbers of insects other than the honey bees and hover flies, which together comprised 92% of all insects recorded (see below in Results, Fig. 7.3), we considered the individual responses of only these two groups in our analyses. To explore possible causes for differences in insect visitation, we fitted General Linear Models (GLMs) using the generalized least squares method with maximum likelihood, which allows for heteroscedasticity (function *gls*, Zuur *et al.*, 2009; Pinheiro *et al.*, 2013), with the mean insect count per unit area as a response variable, ray floret colour, disc floret area, total capitulum area as explanatory variables, and the mean weighted bloom intensity score as a covariate. Due to collinearity among the disc floret area and total

capitulum area, only one was included in a model at a time. The significance of terms was determined using the likelihood-ratio test by dropping individual terms from the full model (Zuur *et al.*, 2009), which is analogous to the full-model t-tests (Whittingham *et al.*, 2006).

The effects of aster species were not included in the above GLMs due to severe unbalancedness of groups (see below in Results, Fig. 7.5). Hence, differences among species were explored using the Kruskal-Wallis one-way test on the subset of species with 10 varieties or more (these were *A. novi-belgii* (n=144), *A. novae-angliae* (n=26) and *A. amellus* (n=17)), followed up *post-hoc* by Wilcoxon-Mann-Whitney pairwise tests adjusted using the Bonferroni method. Similarly, associations between variety attractiveness to insects and attributes relevant to gardening (scored as categorical variables) were also explored using the Kruskal-Wallis test.

Results

Assemblage of insects visiting aster flowers

Of the total of 7125 insect visits to flowers recorded across the study period, 64.3% were hover flies, 28.0% honey bees, 3.3% non-syrphid flies, 2.5% bumble bees, 1.7% butterflies and 0.2% all other insects (Fig. 7.3).

Of the total of 180 bumble bee counts, the majority, 81.1% were 'browns' (main species *Bombus pascuorum*), 11.7% were '2-banded white tails' (main species *Bombus terrestris/lucorum*), 5.6% were 'banded red tails' (main species *Bombus pratorum*, also common, among others, *Bombus lapidarius* males) and 1.7% were 'black-bodied red tails' (main species *B. lapidarius*) (colour groups follow Fussell & Corbet, 1992). A few individuals were queens, probably recently emerged and looking for food between mating flights, or to build up for hibernation.

Of the 118 butterfly counts, 44.9% were small tortoiseshells, *Aglais urticae*, 39.0% were commas, *Polygonia c-album*, 12.7% were red admirals, *Vanessa atalanta*, 2.5% were small whites, *Pieris rapae*, and one individual, 0.8%, was a large white, *Pieris brassicae*.

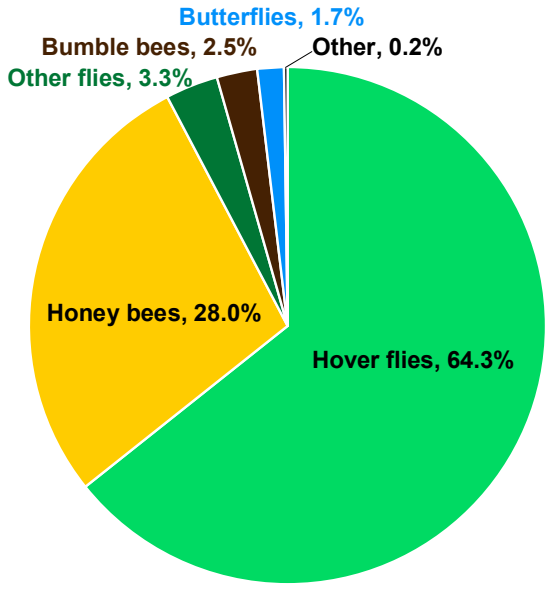


Figure 7.3. Relative abundance of insect groups recorded visiting flowers.

Variation in insect attractiveness among Aster varieties

Only 1% of varieties (n=3) were highly attractive to insects, with >10 per count per m^2 (Fig. 7.4c). Most varieties were unattractive to insects, with 18% (n=40) recording 0 insects and 49% (n=111) recording non-zero values of ≤1 insect per count per m^2. Thirty-two% (n=74) were moderately attractive (1-10 per count per m^2). A similar pattern was seen when looking at either honey bees (Fig. 7.4a) or hover flies alone (Fig. 7.4b), with most varieties visited by either very few, ≤1, insects per count per m^2 (39% & 51%, respectively) or zero insects (48% & 25%, respectively). Measures of attractiveness to honey bees, hover flies and all insects in total for each variety are listed in Appendix 7.1.

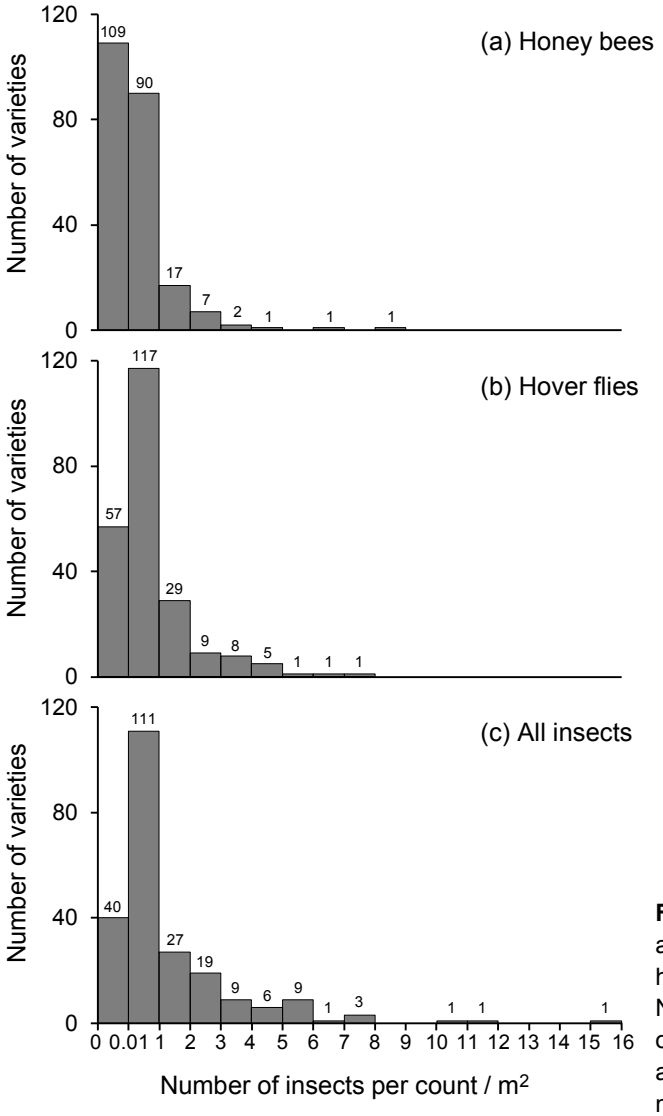


Figure 7.4. Frequency distributions of attractiveness of the 228 Aster varieties to (a) honey bees, (b) hover flies and (c) all insects. Note the first bin (0 - 0.01) is not to scale with other bins and includes only those varieties that attracted exactly zero insects. For names of the most attractive varieties, see Appendix 7.1.

Floral characteristics as explanatory variables of insect visitation

Honey bee and hover fly numbers were significantly affected by the mean weighted bloom intensity score (Table 7.1). However, none of the floral characteristics measured (ray floret colour, disc floret area, total capitulum area) was a significant predictor of insect visitation (Table 7.1). Hover fly visitation significantly increased with both disc floret area and total capitulum area only prior to Bonferroni-correction, but with low explanatory power (Appendix 7.2, McFadden's Pseudo $R^2 = 0.0063$ and 0.0059, respectively).

Table 7.1. P-values of explanatory variables affecting honey bee and hover fly flower visitation in two GLMs. Values in bold are significant at Bonferroni-corrected α-level (0.05 / 2 = 0.025).

	Honey bees per count / m^2		Hover flies per count / m^2	
	L (df)	P-value	L (df)	P-value
Bloom intensity	8.06 (1)	**0.005**	35.75 (1)	**<0.001**
Colour	5.59 (3)	0.133	4.22 (3)	0.239
Disc floret area	0.34 (1)	0.559	4.37 (1)	0.037
Total capitulum area	0.37 (1)	0.545	4.07 (1)	0.044

Differences in insect attractiveness among Aster species

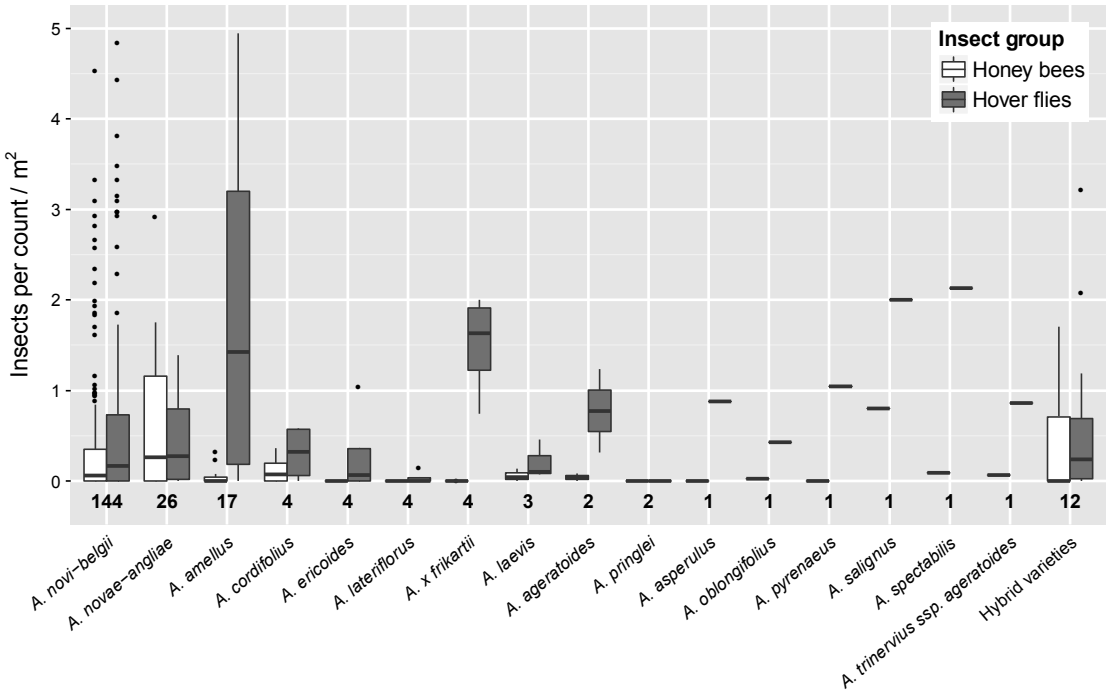


Figure 7.5. Abundance of flower-visiting honey bees (white) and hover flies (grey) per count per m^2 on *Aster* species and hybrid varieties. Numbers of varieties per species are shown below each boxplot pair. Species with at least 10 varieties (*A. novi-belgii*, *A. novae-angliae*, *A. amellus*) were compared statistically (Table 7.2). Other species and hybrids are shown for contextualization and general comparison.

Due to severe imbalance in the numbers of varieties per species, the categorical 'species' variable (Fig. 7.5) was not included as an explanatory variable in the overall GLMs. Hence, comparison of differences among species does not account for confounding variables (bloom intensity, floral colour and size) and should be viewed as a crude analysis. With this reservation, we detected no differences in both honey bee and hover fly visitation to the varieties of *A. novi-belgii vs. A. novae-angliae* (Table 7.2, Fig. 7.5). However, the

varieties of *A. amellus* were significantly more attractive to hover flies, and significantly less attractive to honey bees (Table 7.2, Fig. 7.5).

Table 7.2. Differences among three *Aster* species in attractiveness to honey bees and hover flies

	Honey bees per count / m^2	Hover flies per count / m^2
A. novi-belgii (n=144)		
Median	0.06 (a)	0.18 (a)
IQR	0.36	0.79
A. novae-angliae (n=26)		
Median	0.26 (a)	0.28 (a)
IQR	1.16	0.78
A. amellus (n=17)		
Median	0.00 (b)	1.92 (b)
IQR	0.04	3.28
Kruskal-Wallis test		
K-value (df)	10.05 (2)	10.61 (2)
P-value	0.007	0.005
Wilcoxon-Mann-Whitney test		
A. novi-belgii vs. *A. novae angliae*		
U-value	2255.5	1900
P-value	0.085	0.904
A. novi-belgii vs. *A. amellus*		
U-value	804.5	1801.05
P-value	**0.015**	**0.002**
A. novae-angliae vs. *A. amellus*		
U-value	101.0	331.0
P-value	**0.002**	**0.006**

*Lowercase letters below median values indicate homogeneous subsets based on Wilcoxon-Mann-Whitney pairwise comparison tests, where species sharing a letter are not significantly different at Bonferroni-corrected α-level (0.05 / 3 = 0.017)

Insect visitation and variety attributes relevant to gardening

There were no associations of insect visitation with (i) variety attractiveness from the human perspective (K=1.08, df=2, P=0.583), (ii) ease of cultivation (K=1.27, df=2, P=0.531) and (iii) availability in the UK (K=1.29, df=3, P=0.732) (Fig. 7.6). The same was also true for honey bees alone (attractiveness: K=0.62, df=2, P=0.735, ease of cultivation:

K=0.45, df=2, P=0.799, availability: K=1.16, df=3, P=0.762) and hover flies alone (attractiveness: K=0.89, df=2, P=0.642, ease of cultivation: K=0.51, df=2, P=0.776, availability: K=3.51, df=3, P=0.319) (Appendices 7.3, 7.4).

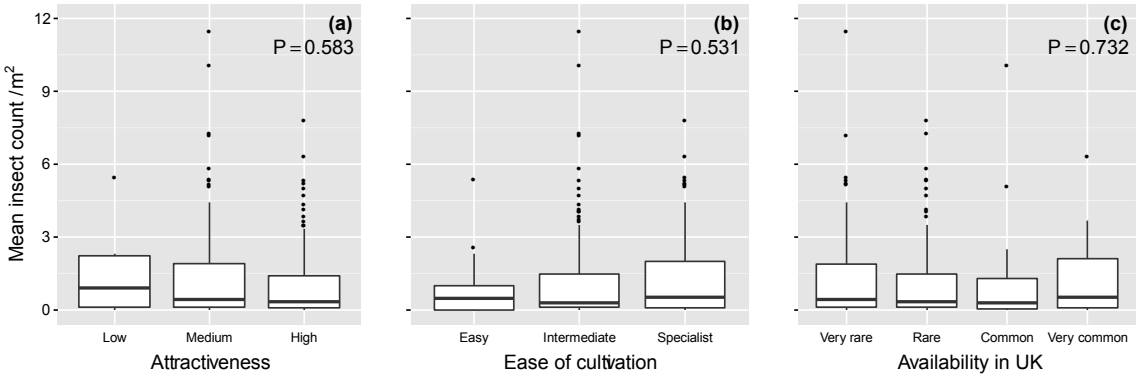


Figure 7.6. Associations of insect visitation with variety attributes relevant to gardening: (a) attractiveness to humans, (b) ease of cultivation and (c) availability in UK.

Discussion

Our data clearly show that only a small proportion of aster varieties are very attractive to flower-visiting insects. However, what determines these differences among the varieties remains unknown. In this study, we detected no effects of floral size or colour on insect visitation. Other plant traits that are likely to play a role include nectar and pollen production per capitulum and the abundance of capitula per plant or per unit area of plant cover. These traits were not measured in our study, but are obvious candidates for investigation in future studies, especially among a sub-set of targeted varieties with high and low numbers of insect visitors. Linked to this question, it would also be valuable to determine what makes the varieties of *A. amellus* more attractive to hover flies and less attractive to honey bees compared to either *A. novi-belgii* or *A. novae-angliae*.

The range of insect attractiveness among aster varieties observed in this study (from 0.00 to 15.20 insects per count per m^2) was very similar to that seen among the 79 varieties of ornamental garden flowers being grown in the Southover Grange garden, a public garden in Lewes, East Sussex, UK (0.00 – 14.34 insects per count per m^2), which we surveyed earlier (Chapter 6). The distribution of attractiveness was also very similar, being highly skewed to the right (cf. Fig. 7.4) meaning that most varieties were

unattractive or poorly attractive (77%) to insects, several were moderately attractive (19%) and very few (4%) were highly attractive. Likewise, we found large differences among dahlias (*Dahlia*) in more limited samples of four varieties (Chapter 5: Garbuzov & Ratnieks, 2014a) and 11 varieties (Chapter 6), where capitulum form appeared to be largely responsible for the differences, with 'open' varieties (single or semi-double) attracting more insects than 'closed' forms (e.g. pompon, cactus or decorative). Thus, this pattern of attractiveness may be common in both ornamental garden plants in general and specific genera or groups of plants in particular. However, unlike dahlia varieties, all aster varieties included in this study had an 'open' capitulum shape, with disc florets easily accessible to insects.

The assemblage of insects visiting aster flowers was similar to that recorded in a recent study on ivy flowers in Sussex, UK, at the same time of year (Chapter 8: Garbuzov & Ratnieks, 2014b), which found that honey bees and both syrphid and non-syrphid flies are very common. One difference is that we saw almost no social wasps (*Vespula vulgaris* or *Vespula germanica*), but it is not clear whether this is because they are not attracted to asters or because they were scarce in the study area or year. *Vespula* can be very common visitors of ivy flowers in autumn in Britain (Jacobs *et al.*, 2010), although their abundance varies greatly on a local scale and among years (Chapter 8: Garbuzov & Ratnieks, 2014b) and appears to exhibit cyclic dynamics (Archer, 1985). In contrast, bumble bees were scarce probably because their annual colony life cycle comes to an end in autumn (Prŷs-Jones & Corbet, 1991). Butterflies were also few in number, probably because they are less numerous and spend a relatively low proportion of their time foraging, in contrast to social bees, many of whom are common and spend most of their time foraging to provision for the colony. The low proportion of butterfly counts (<2%) is also similar to that recorded in earlier ornamental plant surveys in Falmer (Chapter 5: Garbuzov & Ratnieks, 2014a) and Lewes (Chapter 6), East Sussex, and appears typical for England.

Asters frequently feature in lists of wildlife friendly plants. In many lists, asters are simply recommended under the all-encompassing name of "asters" (e.g. Vickery, 1998; Baines, 2000; Hooper & Taylor, 2006). Gardening advice for the general public often

comes from gardeners who host TV programmes. The same people often write gardening advice articles for newspapers and magazines. For example, in the UK, Monty Don, who is a well-known expert gardener and presenter of gardening programmes, commented in an article written for a national newspaper that asters are "always wonderful for attracting insects" (Don, 2011). However, as shown in this study, such recommendations are inaccurate and simplistic, as they ignore the tremendous variation among the varieties within this group. Sometimes recommendations are narrowed down to a particular species, such as *A. novi-belgii* or *A. novae-angliae* (e.g. Lavelle & Lavelle, 2007; RHS, 2011), but our study showed that even within a species varieties are still hugely variable. In a few cases, recommendations go as far as specifying a particular variety, e.g. *A.* × *frikartii* 'Mönch' (CCW, 2008; RHS, 2011), showing that there is a demand for concrete and specific information. Our data, however, show that 'Mönch' is relatively unattractive compared to other varieties (Appendix 7.1).

Our study provides an example of a national plant collection being used to gather useful data. Although even national collections cannot be expected to include all possible varieties of a particular plant group, they will normally provide a comprehensive range of species or varieties and, therefore, present a valuable resource for research. The methodology used in our study is not difficult and could easily be uses by other researchers. It is also suitable for data collection via 'citizen science' (Dickinson *et al.*, 2010). In particular, it is straightforward to learn how to count insects and to identify them to broad taxonomic categories, and to measure patch sizes and score bloom intensity. In addition, in national collections varieties are typically grown in labelled patches or beds, which aids in the generally difficult or often impossible task of variety identification.

A novel feature of our study was the assessment of plant attributes relevant to gardening and their relationship to flower visitation by insects. Our data show that varieties more attractive to insects are not, on average, less attractive to humans, more difficult to grow or more difficult to obtain. The price of varieties sold in the Picton Garden was either £5.90 or £6.90. However, this difference was solely due to the size of

the pot they were sold in. Therefore, helping flower-visiting insects in gardens by choosing insect-attractive aster varieties is a no-cost option for gardeners and one that need not involve making any sacrifices in terms of garden beauty or gardening effort.

Using our dataset, a few varieties that are particularly good in multiple respects can be provisionally recommended to gardeners, growers and garden centres. Most of the best varieties near the top of the table (Appendix 7.1) are varieties of *A. novi-belgii*. However, this is not significantly disproportional to their overall representation in the collection, as *A. novi-belgii* had, by far, the highest number of varieties in the collection (63%, n=144 of 228, see Fig. 7.5). These include, for example, 'Alice Haslam' and 'Dandy'. But also varieties, such as 'Alderman Vokes', 'Little Man in Blue' or 'Anneke', that suffer from lack of availability in the UK, being categorized as either 'rare' or 'very rare'. It is also worth noting that, in the gardening world, *A. novi-belgii* has a reputation for being susceptible to mildew, in contrast to *A. novae-angliae*, which is regarded as largely pest and disease free (Don, 2011), although, as far as we are aware, it has not been rigorously examined in research.

Our dataset should be valuable in providing marketing opportunities for horticulturalists to propagate insect-friendly varieties, for gardeners in buying varieties, and for gardening organizations in promoting varieties. But we also suggest that the results pertaining to particular varieties should be verified by further observations and tests before any are highly promoted. This is because, although the overall pattern of insect visitation among the 228 varieties is robust, variety-specific results may have been subject to idiosyncratic effects of patch location on a fine scale. In addition, the identity of a variety may sometimes not match the original due to clonal divergence or simply a labelling error, and so may need to be verified, as is done with cultivars of economically important crops, such as grapevines, olives, apples, sunflowers and many others (Zhang *et al.*, 2005; Mackay *et al.*, 2008; Evans *et al.*, 2011). Indeed, misidentification due to a labelling error is presumably likely in public gardens or garden centres, but not in national collections, which is another advantage of these collections for carrying out research comparing varieties.

Research Chapters

Part 3: Attractiveness of Urban Wild Flowers to Flower-Visiting Insects

Chapter 8

Ivy: an underappreciated key resource to flower-visiting insects in autumn

Mihail Garbuzov, Francis L. W. Ratnieks

Abstract

Ivy (*Hedera helix* and *H. hibernica*) is a common autumn-flowering plant found in Europe, North Africa, Macaronesia and Asia. Here, we use five complementary approaches (pollen trapping, nectar refractometry, local and regional surveys of insects foraging on ivy flowers, local survey of ivy abundance) to evaluate its importance to the honey bee (*Apis mellifera*) and other flower-visiting insects in Sussex, England. Pollen trapping at six hives in two locations showed that an average 89% of pollen pellets collected by honey bees in the autumn were from ivy. Observations of foraging honey bees on ivy showed that ivy nectar is an even greater target than pollen, as 80% were collecting only nectar. Refractometry of samples from ivy flowers and from honey bees foraging on ivy showed that ivy nectar is rich in sugar, 49% w/w. Surveys showed that the main insect taxa foraging on ivy were honey bees (21%), bumble bees (*Bombus* spp., 3%), ivy bees (*Colletes hederae*, 3%), common wasps (*Vespula vulgaris*, 13%), hover flies (Syrphidae, 27%), other flies (29%) and butterflies (4%). The surveys also showed significant temporal and spatial variation in taxon abundance and proportion. A survey showed that ivy was very abundant on a small scale in both rural and urban areas, being present in 10/10 and 6/10 0.2×0.2 km samples within two 4×4 km areas respectively. The results show that ivy should probably be considered a keystone species with a high value in the conservation of flower-visiting insects in autumn.

Introduction

Honey bees (*Apis mellifera*) and other pollinating insects have declined since WW2 with a major factor being the reduction in flower abundance (Biesmeijer *et al.*, 2006; Carvell *et al.*, 2006; Goulson *et al.*, 2008b; Potts *et al.*, 2010a). Nevertheless, the relative importance of different plant species in the diet of different pollinating insects is not fully known. Previous work has shown, for example, that white clover (*Trifolium repens*), heather (*Calluna vulgaris*), bramble (*Rubus* spp.), oilseed (*Brassica* spp.) and hawthorn (*Crataegus* spp.) are among the most important sources of nectar and pollen for honey bees in the UK (Roberts, 1994; Beekman & Ratnieks, 2000). Similarly, heather and red and white clovers (*Trifolium pratense* and *T. repens*) and are some of the most important floral resources for bumble bees (Goulson *et al.*, 2005). Nevertheless, the importance of different plant species in the diet of pollinators is dynamic and shows seasonal variation (Visscher & Seeley, 1982; Roubik & Villanueva-Gutiérrez, 2009). Knowledge of the importance of plant species to animals that rely on them can be useful in informing land management, environment policy and conservation action (Dicks *et al.*, 2010).

Research on honey bee foraging has shown that in Sussex (southern Britain) the average foraging distance of honey bees, as determined by decoding waggle dances reduces from summer (July and August, c. 4 km) to autumn (September and October, c. 2 km) (Couvillon *et al.*, 2014a), suggesting that floral resources become more available. We hypothesised that this increase in floral resource abundance is due to the blooming of ivy (*Hedera* spp.). Ivy is a common and widespread native plant found throughout Britain in both rural and urban areas and blooms mainly in September and October (Metcalfe, 2005). Ivy bloom can be prolific, although it is often overlooked, as the flowers are small (5 mm) and inconspicuous, lacking bright petals.

The ivy genus, *Hedera*, comprises c. 16 species distributed throughout Europe, North Africa, Macaronesia and Asia. The two British species are *H. helix* and its tetraploid daughter species *H. hibernica* (Ackerfield & Wen, 2003). Both are common and have overlapping distributions throughout most of the British Isles, although *H. hibernica* is

considered under-recorded (Metcalfe, 2005). Both species are woody climbers with almost identical morphology (McAllister & Rutherford, 1990). The juvenile form has lobed leaves and creeps over the ground, but climbs vertically on substrates, such as tree trunks, cliffs, walls and buildings when mature, aged 10 years or more, and produces ovate leaves and flowers (Clark, 1983).

The aim of this study was to assess the local abundance of ivy and its importance as an autumn food source to honey bees and other flower-visiting insects in both urban and rural areas by determining: (i) the proportion of pollen pellets collected by honey bee foragers from ivy during its main flowering period, (ii) the sugar concentration in ivy nectar and the proportion of honey bee and bumble bee (*Bombus* spp.) foragers collecting nectar versus pollen, (iii) the local and (iv) regional assemblage and relative abundance of ivy flower-visiting insects and (v) the local distribution and abundance of ivy. By collecting these five complimentary datasets, we are able to build a significantly more comprehensive picture than previous studies, which were based either on the analysis of honey bee pollen pellets (Coffey & Breen, 1997) or counts of insects foraging on ivy flowers (Vezza *et al.*, 2006; Ollerton *et al.*, 2007; Jacobs *et al.*, 2010).

Methods

Pollen collection and identification

Pollen was collected from 6 honey bee (A. mellifera) observation hives. Three were at the rural location (Laboratory of Apiculture & Social Insects, University of Sussex, Brighton, UK; latitude: 50.863889, longitude: -0.083830386) and three at the urban location (Dorothy Stringer High School, Brighton, UK; latitude: 50.849370, longitude: -0.14167996). The two locations are 4.5 km apart.

Pollen from each hive was obtained by placing a pollen trap (5.0 mm plastic mesh; E.H.Thorne, UK) onto the end of each hive's 40 mm diameter entrance tube. The mesh

knocks pollen pellets from the pollen baskets of returning foragers as they pass through. Pollen was collected approximately weekly on days with good foraging weather during the main ivy flowering period, from 13 September to 15 October 2011, 09.00 hours–17.00 hours local time. Each sample was the group of pollen pellets collected from one hive on one day. After collection and prior to identification, pollen samples were stored at -20 °C for 3 weeks.

Pollen was identified dichotomously as either ivy or non-ivy. In most cases, the daily sample from a hive was abundant and we analysed 50 pellets. Occasionally (6 of 29), the sample was less than 50 pellets and all were identified. A further 4 samples returned 0 pellets. All pellets were of a single colour indicating that the pollen came from a single plant species, as expected given that the frequency of mixed honey bee pollen pellets is very low [0.05% in Wales, UK (Percival, 1947), <0.01% in Caldén, Argentina (Andrada & Tellería, 2005)]. In addition, when examining pollen under the microscope, we never saw more than one pollen type per pellet.

A small amount of pollen from each pellet, comprising several hundred grains, was made into a temporary slide under a cover slip with water and examined under bright field using Zeiss Axiophot microscope (Carl Zeiss, Oberkechen, Germany) at 400× magnification. Ivy pollen was identified by reference to a suite of characteristic features described by Van Helvoort and Punt (1984) and to samples collected locally. In practice, a combination of shape and size made it easy to recognise.

Measurements of sugar concentration in ivy nectar

Total sugar concentration (% w/w, °Brix) was measured from 10 ivy flowers individually on one warm (daytime average 14 °C) and sunny day (4 October 2012) from a patch near peak bloom in Falmer, using a handheld refractometer designed for small volumes (Model 45–81, Bellingham & Stanley, Tunbridge Wells, UK). As the nectar is secreted on the surface of an exposed floral disc, it was transferred onto a refractometer prism by smearing the disc surface against the prism surface. In addition, sugar concentration was

measured from the crop contents of 10 honey bee workers foraging on the same patch of ivy at the same time. Crop contents were obtained by chilling captured bees and gently pressing on the abdomen to cause regurgitation of a small volume. Test bees were not killed and were then released.

Survey of ivy flower visitors on a small scale in Falmer

Insects on ivy flowers were surveyed in five locations within Falmer village, which neighbours the University of Sussex campus (latitude: 50.865006, longitude: -0.078547061) and is c. 500 m from the experimental apiary at the Laboratory of Apiculture & Social Insects. The locations were chosen to have abundant flowering or soon-to-flower ivy and were 60–380 m apart.

Surveys took place at approximately weekly intervals corresponding with the main 2011 ivy flowering period on the following dates: 15, 23, 30 September and 10, 14 October. The surveys were repeated in 2012 on 21 September and 6, 10, 14 October. Temperature was recorded on each day at 15 minutes intervals from 09:00 to 17:00 BST using a weather station (Vantage Pro 2, Davis, CA, USA) located at the Laboratory of Apiculture & Social Insects; the means of these 33 records per day were used to produce a daytime average in subsequent analyses. The 2011 surveys were made during good weather. That is, sunny, warm (range of daytime averages 13.7–23.9 °C) and with low or modest wind (range of daytime averages 0.1–2.6 m s^{-1}). In 2012, we also aimed to make surveys on only good days. Nevertheless, poor weather meant that the surveying temperature range was lower (9.6–15.0 °C), but still not windy (0.4–0.8 m s^{-1}). On each day, the ivy bloom intensity at each location was quantified by assigning it a score 0 (absence of bloom), 1 (<⅓ of maximum), 2 (⅓–⅔ of maximum) and 3 (full bloom, >⅔ of maximum) (after Anderson & Hubricht, 1940).

Insects visiting ivy flowers were quantified using a snapshot count method, in which the insects foraging in a defined patch of flowers are recorded near instantaneously (<10 s) by eye. On each surveying day each of the five locations had 10 counts, each in an

area of 1 m^2 of flowering ivy. Each count used the same general area per location but not the same precise area of flowers. Counts were made in sequence by walking from one location to the next, such that there was an interval of 10–20 minutes between counts at the same location, which minimized the chance of recording the same insect twice on the same foraging visit to a patch. As the main aim of the counts was to determine the relative abundance of insect taxa, the exact sizes of the areas surveyed were not critical.

All ivy flower visitors recorded were insects and were identified to taxa as follows: (i) honey bee, *A. mellifera*, (ii) bumble bees, *Bombus* spp., (iii) ivy bee, *Colletes hederae*, (iv) common wasps, *Vespula vulgaris*, (v) hover flies, Diptera: Syrphidae, (vi) other flies, non-syrphid Diptera, (vii) butterflies, Lepidoptera (Fig. 8.1). The presence or absence of pollen in the pollen baskets of *A. mellifera* and *Bombus* spp. was also noted.

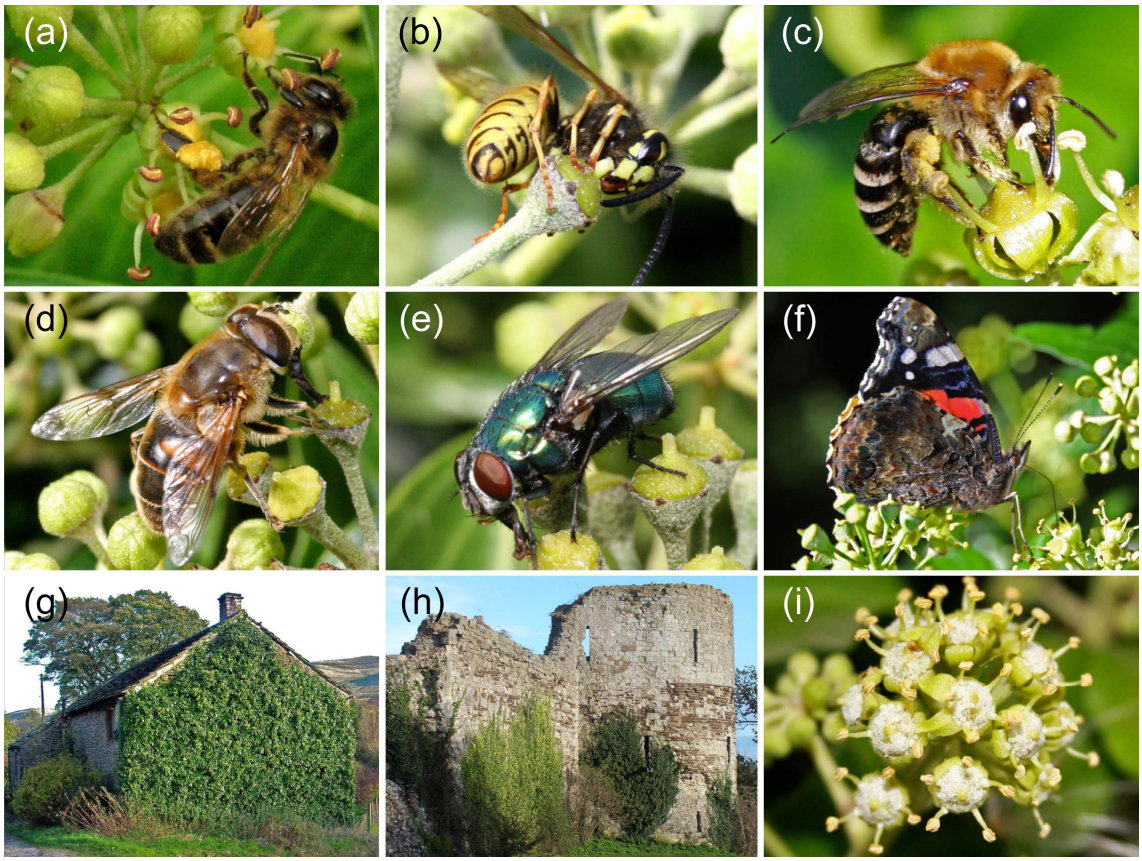


Figure 8.1. Insects on ivy flowers: (a) honey bee (*Apis mellifera*) worker with a pollen load in its basket, (b) common wasp (*Vespula vulgaris*) ♂, (c) ivy bee (*Colletes hederae*) ♀, (d) hover fly (*Eristalis tenax*, Syrphidae, honey bee mimic), (e) green bottle fly (*Lucilia* sp., Calliphoridae) and (f) red admiral butterfly (*Vanessa atalanta*). (g) Mature ivy climbing over the wall of a house in Derbyshire, northern England, UK and (h) the Pevensey castle, southern England, Sussex, UK. (i) Ivy flowers with nectar sugars turned into white crystals due to evaporation of water.

Survey of ivy flower visitors over a wider area in Sussex

In addition, insects on ivy flowers were surveyed on a larger scale in 8 locations within 30 km wide area in Sussex, UK in 2012 (Fig. 8.4). The locations were paired such that one urban and one rural location (within c. 4 km of each other) were surveyed at each of 4 general locations. Two general locations were on chalk (alkaline) soil type (Brighton, Seaford) and two were on Wealden group strata (acidic: mudstone, siltstone and sandstone) soil type (Uckfield, Hailsham) (British Geological Survey, 2012). Surveys were made at intervals broadly corresponding with the early (22 September), middle (30 September–6 October) and late (14–16 October) ivy flowering periods. In each survey period exactly 100 individual insects were recorded in each location. The insects were identified to the taxa in the same way as in the Falmer survey, with the exception that 11 sphecid wasps (*Mellinus arvensis*) were added to the 'wasps' group. These were only seen at the Hailsham general location.

Survey of ivy local abundance

The abundance of ivy was estimated in two 16 km^2 (4 × 4 km) areas (Fig. 8.5). One, approximately centred on the Laboratory of Apiculture & Social Insects, was mainly rural and comprised mainly agricultural land. The other, centred approximately on the Dorothy Stringer High School in the city of Brighton, was urban. Each was subdivided into 400 200 × 200 m sub-areas, 10 of which were randomly chosen and surveyed. Each sub-area was surveyed on foot and the abundance of ivy determined by approximating its growth form to either a surface, for example, when growing over ground, walls, fences or trees (to the nearest 1 m^2) or volume, when taking a shrub-like form (to the nearest 1 m^3). A small proportion of each area (11 ± 2% per urban subarea, 4 ± 3% per rural sub-area) was not surveyed due to inaccessibility (e.g. private back gardens). This non-sampled area

was measured by analysing Google satellite images using the software ImageJ 1.45s (National Institute of Health, Bethesda, MD, USA).

Statistical analyses

The relationships between the proportion of ivy pollen pellets, sampling date and location were analysed using Generalised Linear Mixed Model (GLMM) (Zuur *et al.*, 2009), where proportion of ivy pollen was included as the response variable, sampling date and location as fixed effects and hive as a random effect to account for non-independence of data within hives. Arcsine square root transformation was applied to the proportion data prior to the analysis. The optimal structure of random components was determined by altering the model in steps by allowing (i) the intercept and (ii) the intercept and slope to vary. Subsequently, the significance of each step was determined from the change in the fit of the model (measured as -2 log-likelihood ratio) in a χ^2 distribution with appropriate degrees of freedom. The relationships between the number of insect visitors per count, survey date, bloom intensity and temperature were similarly analysed using GLMM, where the number of insects was included as the response variable; survey date, bloom intensity and temperature as fixed effects and location as a random effect. One GLMM was run for each taxon, hence significance of P-values was judged against the Bonferroni-corrected α-level (0.05/6 in 2011, 0.05/7 in 2012).

Each sample of 100 insects from each of 8 locations across Sussex was treated as a 'community' for the purposes of the analysis. Permutational multivariate ANOVA (PERMANOVA) (Anderson, 2001; Anderson *et al.*, 2011) was used to determine how much (or if any) variation in community structure (expressed as a matrix of Bray–Curtis dissimilarity indices between individual 'communities') is explained by land use (urban or rural), soil type (chalk or Wealden group) or sampling period (early, middle or late).

All statistical analyses were performed in R v.2.15.2 (R Development Core Team, 2012). GLMMs were run using function *lme* (package *nlme*, Pinheiro *et al.*, 2012).

PERMANOVA was run using function *adonis* (package *vegan*, Oksanen *et al.*, 2012). All values reported are means ± standard error, unless otherwise stated.

Results

Ivy pollen collection by the honey bee

From 13 September to 15 October 2011 a mean of 89.0% (SD = 12.5%, SE = 2.3%, n = 29) of the pollen pellets collected by *A. mellifera* were ivy with a range of 58–100% per sample (Fig. 8.2). Percentages did not vary among sampling dates (L = 0.376, d.f. = 1, P = 0.540), nor between the urban and the rural location (L = 0.375, d.f. = 1, P = 0.541), and there was no interaction between sampling date and location (L = 0.319, d.f. = 1, P = 0.572).

The model fit was not significantly improved by the addition of hive factor as either a random intercept (L = 0.282, d.f.=1, P = 0.594) or a random intercept and slope (L = 5.472, d.f.=9, P = 0.791), indicating that there were no differences among the hives.

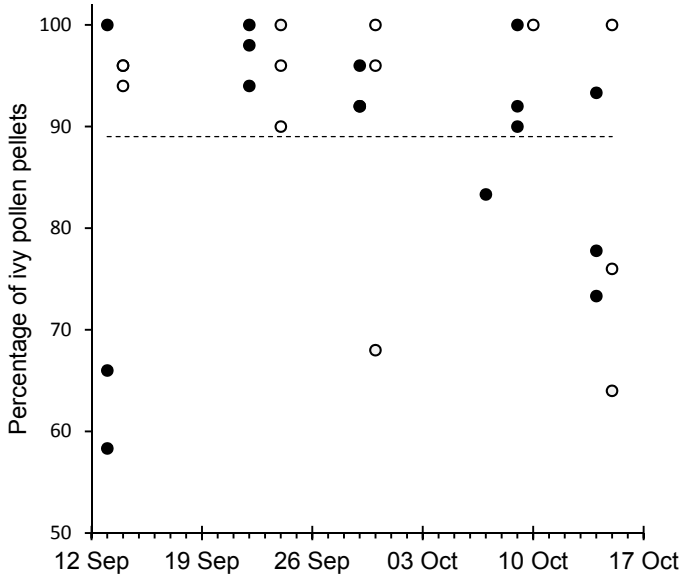


Figure 8.2. Pollen collection by the honey bee from ivy during its main flowering period. Each data point is % of ivy in a sample collected on one day from one hive located either at the University of Sussex (●, closed circles) or the Dorothy Stringer School (○, open circles). Dashed line shows the overall mean of 89.0%.

Sugar concentration in ivy nectar

The sugar concentration in nectar collected from ivy flowers was 49.2 ± 1.4% (n = 10) and was not significantly different from that in crop contents of honey bees foraging on the same flower patch, 49.5 ± 1.5% (n = 10) (t-test, t18 = -0.146, P = 0.886), strongly suggesting that the sole content of bee crops was ivy nectar. The overall mean sugar concentration in ivy nectar was thus estimated at 49.3 ± 1.0%.

Survey of ivy flower visitors on a small scale in Falmer

The mean numbers of insects in each taxon and their relative proportions are shown in Fig. 8.3. In 2011, over half the flower visitors came from just two species, the common wasp, *V. vulgaris* (27.5%) and the honey bee, *A. mellifera* (27.2%; 85% of all bees). Bumble bees, *Bombus* spp., comprised 4.7% (15% of all bees), and no other bees were seen. True flies (Diptera) comprised 37.8%, of which over half (52.7%, but 19.9% of all insects) were hover flies (family Syrphidae). Lepidoptera were 2.7% of all insects recorded.

In 2012, in contrast, Diptera were the most abundant group comprising 62.2% of all insects, of which about a third (36.4%, but 22.7% of all insects) were hover flies. *Apis mellifera* were 22.7% (78% of all bees) and *Bombus* spp. were 3.5% (12% of all bees). Ivy bees, *C. hederae*, which were not seen in 2011, were 2.9% (10% of all bees). The relative abundance of *V. vulgaris* dropped considerably to only 3.5%. Lepidoptera were 5.2% of all insects.

In 2011, from a total of 172 *A. mellifera* workers and 30 *Bombus* spp. workers recorded, 16% and 27%, respectively, had pollen in their baskets. Twenty-eight of 30 *Bombus* spp. individuals were 'two-banded white tails' (*B. terrestris L./lucorum* colour group) and 2 were 'browns' (*B. pascuorum* colour group) (after Fussell & Corbet, 1992). Of the 17 Lepidoptera recorded, all were butterflies (16 red admirals, *Vanessa atalanta*; 1 speckled wood *Pararge aegeria*).

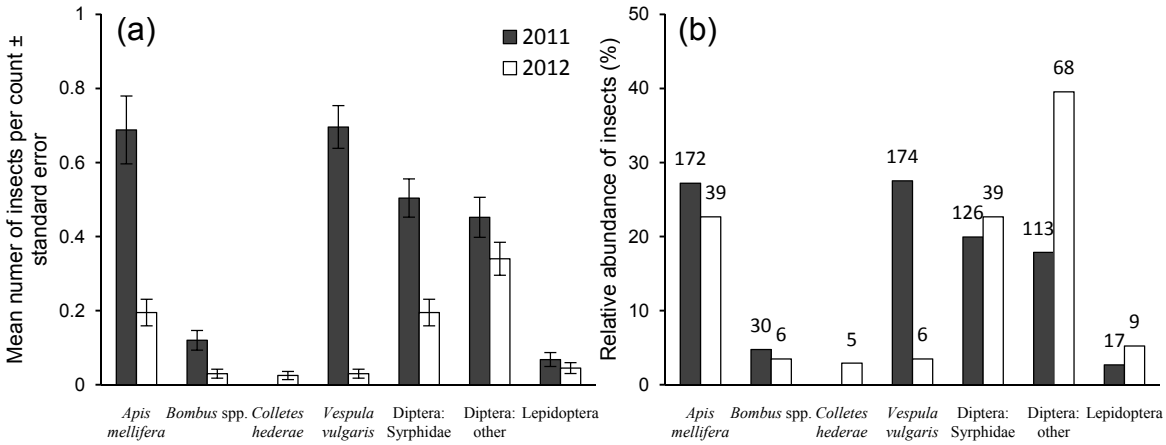


Figure 8.3. Survey of ivy flower visitors on a small scale in Falmer. Mean numbers of individuals ± standard error (a) and relative abundance (b) of each insect taxon recorded on ivy flowers in 5 locations within Falmer village in 5 observation days between 15 September and 14 October (2011, grey bars) and 4 observation days between 21 September and 14 October (2012, white bars). The values above bars (b) are the total numbers per taxon (total 632 in 2011, 172 in 2012).

In 2012, from a total of 39 *A. mellifera* workers and 6 *Bombus* spp. workers recorded, 28% and 0%, respectively, had pollen in their baskets. Three of 6 *Bombus* spp. individuals were 'two-banded white tails' and 3 were 'browns' (Fussell & Corbet, 1992). Of the 9 Lepidoptera recorded, all were butterflies (8 red admirals, *V. atalanta*; 1 comma, *Polygonia c-album*).

Both *V. vulgaris* and *Vespula germanica* are active in Britain in September and October. Nevertheless, all individuals that we were able to observe closely in both years were identified as *V. vulgaris*. No hornets (*Vespa crabro*) were seen even though they occur locally and are still flying in early autumn (FR pers. obs.).

The significance of the relationships between the number of insects per count and date, bloom intensity and temperature for each taxon are shown in Table 8.1. In 2011, all taxa except *V. vulgaris* were significantly more abundant with higher bloom intensity. *Apis mellifera*, non-syrphid Diptera and Lepidoptera showed a significant trend over sampling date; however, the very low slope estimates (0.054, -0.023 and 0.006 respectively) make this trend negligible. Furthermore, only *A. mellifera* was slightly more abundant with warmer temperatures (b = 0.176).

In contrast, in 2012, no taxon showed a significant relationship with bloom intensity. The abundances of Syrphidae and Lepidoptera were significantly related to

sampling date, but the low slope estimates (0.026 and 0.012 respectively) again make this relationship of little importance. Furthermore, Syrphidae and Lepidoptera were slightly more abundant with warmer temperatures, but the slope estimates were again very low (0.087 and 0.045 respectively).

Table 8.1. Survey of ivy flower visitors on a smaller scale in Falmer. P-values (and slope estimates where relationship is significant) of explanatory variables and random location factor for the number of insects per snapshot in multilevel GLMMs for each taxon. Values in bold are significant at Bonferroni-corrected α-level (0.05 / 6 in 2011, 0.05/7 in 2012)

	Apis mellifera	*Bombus* spp.	*Colletes hederae*	*Vespula vulgaris*	Diptera: Syrphidae	Diptera: all other	Lepidoptera
2011							
Date	**<0.001 (0.054)**	0.546	N/A	0.700	0.059	**<0.001 (-0.023)**	**0.001 (0.006)**
Bloom intensity	**<0.001 (0.875)**	**<0.001 (0.192)**	N/A	0.156	**<0.001 (0.537)**	**0.001 (0.228)**	**0.001 (0.074)**
Temperature	**<0.001 (0.176)**	0.060	N/A	0.900	0.463	0.463	0.029*
2012							
Date	0.016*	0.382	0.074	0.092	**0.001 (0.026)**	0.784	**<0.001 (0.012)**
Bloom intensity	0.110	0.048*	0.009*	0.858	0.869	0.011*	0.383
Temperature	0.156	0.077	0.549	0.583	**0.007 (0.087)**	0.387	**<0.001 (0.045)**

* P-value significant before, but not after the Bonferroni correction

Survey of ivy flower visitors over a wider area in Sussex

Variation in structure of ivy flower-visitor communities was not significantly related to either soil type (chalk vs. Wealden group, F = 3.219, d.f.=1, P = 0.061), land use (urban vs. rural, F = 2.864, d.f.=1, P = 0.058) or sampling period (early vs. middle vs. late, F = 1.641, d.f.=2, P = 0.183). There were also no significant interactions (all P > 0.05). The general location, however, had a significant relationship with community structure (F = 6.563, d.f.=2, P = 0.002), explaining 34% of variation among community samples (R^2 = 0.336). All communities were dominated by Diptera (including Syrphidae), which on average comprised 67.5% of all insects (Table 8.2). Notable differences among communities include the highest relative proportion of *A. mellifera* in Hailsham (32.3% compared to mean 14.3%), the highest relative proportion of *C. hederae* in Seaford (16.5% compared to mean 5.4%), the highest relative proportion of wasps *V. vulgaris* in Uckfield (18.8% compared to mean 7.3%) and the highest relative proportion of butterflies in Brighton (9.0% compared to mean 5.0%) (Fig. 8.4; Table 8.2).

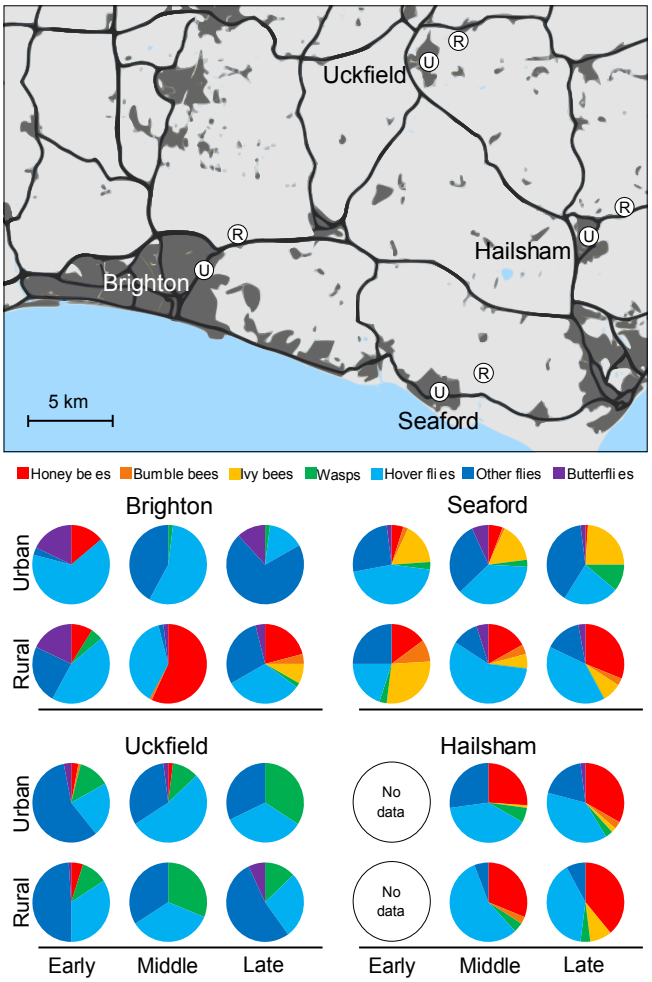


Figure 8.4. Survey of ivy flower visitors over a wider area in Sussex. Community structures of ivy flower-visiting insects in 8 locations, 1 urban (U) and 1 rural (R) within each of 4 general locations sampled at periods broadly corresponding to the early (22 September), middle (30 September–6 October) and late (14–16 October) ivy flowering periods in 2012. The 4 general locations represent alkaline chalk (Brighton, Seaford) and acidic Wealden group (Uckfield, Hailsham) soil type.

Survey of ivy local abundance

In the mainly rural area ivy was recorded in 6 of 10 40,000 m^2 sub-areas with a mean of 79 ± 42 m^2 and 5 ± 5 m^3 per sub-area, comprising c. 0.2% of the total area (Fig. 8.5; Table 8.3). In the mainly urban area, ivy was recorded in all 10 sub-areas with a mean of 390 ± 98 m^2 and 39 ± 14 m^3 per sub-area, comprising c. 1% of the total area. On average, 4 ± 3% and 11 ± 2% of each sub-area was not surveyed due to inaccessibility in the rural and urban areas, respectively. In both areas, ivy was found growing over the ground, walls, buildings, fences, hedges and trees, and in one sub-area even over tombstones. Ivy can, therefore, climb over a wide range of substrates, both natural and man-made (Fig. 8.1g,h). Nevertheless, ivy was absent from agricultural fields, which was the only habitat type in the survey where it was not found.

Table 8.2. Survey of ivy flower visitors over a wider area in Sussex. Percentages of taxa in ivy flower visiting communities in 4 general locations surveyed. White columns are main taxa used in the community structure analysis; grey columns are sub-units showing detail of % breakdown of the respective main taxa

General location	*Apis mellifera*	% *Apis mellifera* with pollen	*Bombus* spp	% *Bombus* spp with pollen	*Bombus terrestris*	*Bombus pascuorum*	*Colletes hederae*	Total wasps	*Vespula vulgaris*	*Mellinus arvensis*	Diptera: Syrphidae	Diptera: all other	Total Lepidoptera	*Vanessa atalanta*	*Polygonia c-album*
Brighton	16.8	22.7	0.8	0.0	100.0	0.0	1.3	1.8	100.0	0.0	41.7	28.5	9.0	85.2	14.8
Seaford	12.5	12.0	3.2	16.7	83.3	16.7	16.5	3.3	100.0	0.0	37.0	24.3	3.2	94.7	5.3
Uckfield	10.0	6.7	0.2	0.0	100.0	0.0	0.0	18.8	100.0	0.0	34.2	43.0	2.2	92.3	7.7
Hailsham	32.3	36.4	1.5	0.0	66.7	33.3	3.0	4.3	35.3	64.7	43.5	15.0	0.5	100.0	0.0
Grand mean	14.3	33.0	1.4	10.5	80.0	20.0	5.4	7.3	93.2	6.8	38.7	28.9	4.0	88.6	11.4

Discussion

Ivy abundance and role in honey bee diet

Our results show the ivy pollen is very prominent in the honey bee diet during September and October, averaging 89.0% of pollen pellets (Figs. 8.1a, 8.2). This likely reflects the fact that relatively few other plant species in Britain flower during this time. Our results also show that, in addition to being widespread throughout Britain on a broad scale (10 × 10 km grid, Metcalfe, 2005), ivy is also abundant on a local scale (Fig. 8.5; Table 8.3). Given that honey bees can forage up to 10–12 km from the hive (Beekman & Ratnieks, 2000), it is likely that a honey bee colony in Britain would never be out of range of ivy. In agreement with this, Coffey and Breen (1997) found that in Ireland ivy was one of the dominant pollen sources in September and the only source remaining in October.

Pollen is the sole source of proteins, lipids, vitamins and minerals for developing honey bee brood and young adults (Herbert, 1992). Indeed, pollen foraging is directly stimulated by brood rearing (Vaughan & Calderone, 2002). In temperate regions, honey bees are still rearing brood in September and October, while the dwindling amounts of pollen availability at the end of season provide a cue for colony transition into a broodless state for overwintering (Mattila & Otis, 2007). In colonies at the Laboratory of Apiculture & Social insects, there is considerable brood rearing in September. This diminishes through October and by November there is rather little brood in most colonies (FR pers. obs.). The amount of pollen stored in the comb is maintained around a homeostatic set-point (c. 1 kg in

strong colonies) (Fewell & Winston, 1992; Seeley, 1995). Hence, the pollen collected in late season and stored over winter is used to commence brood rearing in the following season much earlier (typically in late winter) than the weather conditions permit foraging (Seeley & Visscher, 1985).

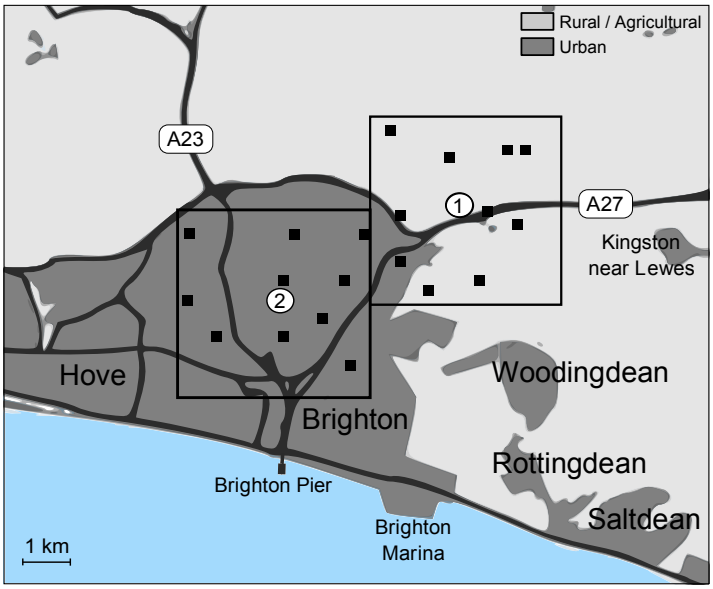


Figure 8.5. Survey of ivy local abundance. Map showing the two 4 × 4 km study areas: rural, centred approximately on the Laboratory of Apiculture & Social Insects at the University of Sussex (1) and urban, centred approximately on the Dorothy Stringer High School (2). Ivy abundance was recorded by surveying on foot in the ten randomly selected 200 × 200 m sub-areas (black) within each area.

Table 8.3. Survey of ivy local abundance. Amount of ivy (mean ± standard error) per 200×200 m sub-area approximated either to an area cover (m^2) or volume (m^3) in two 4×4 km areas

Area	Ground* (m^2)	Walls/fences (m^2)	Hedges (m^2)	Trees (m^2)	Shrub-like form (m^3)	Approximate surface area of voluminous shrub-like form (m^2)	Total area (m^2)	Proportion not surveyed
Area 1: rural (around Laboratory of Apiculture & Social Insects)	9 ± 9	11 ± 7	9 ± 7	50 ± 24	5 ± 5	17 ± 16	96 ± 43	4 ± 3%
Area 2: urban (around Dorothy Stringer High Schol)	43 ± 15	129 ± 42	8 ± 2	211 ± 64	39 ± 14	99 ± 32	489 ± 156	11 ± 2%

* All ivy growing over ground was juvenile, while >90% of ivy on all other substrates and all ivy in shrub-like form was mature

Although ivy pollen is important, our data indicate that ivy nectar is of even greater importance, given that 79.7% of honey bees (also 94.6% of bumble bees) foraging on ivy flowers did not have pollen in their baskets. In line with this, Greenway *et al.* (1975) reported that in Ireland a significant amount of the winter honey stores were made from ivy nectar. The total sugar concentration in ivy nectar recorded in this study was 49.3% (w/w), which is considerably higher than that reported previously in Italy, 3.5–7.5% (Vezza *et al.*, 2006) and Britain, 10–11% (Wykes, 1953) (values reported in different units converted to % w/w as recommended by Bolten *et al.* (1979)). The difference observed

between our data and previous studies may be caused by both nectar being diluted by other water sources, such as dew and rain, and being concentrated by evaporation, which is facilitated by the open structure of flowers, where the nectar is secreted on the exposed surface of the floral disc. Indeed, it is sometimes possible to observe flowers where the sugar concentration has reached nearly 100%, turning into solid crystals (Fig. 8.1i). Seeley (1995) reported a wide range of nectar sugar concentrations in the crops of returning honey bee foragers, with 49.3% not unusually high. In addition, it compares favourably with that found in plant species well-known to be attractive to the honey bee, such as bramble, *Rubus fruticosus* (15–39%) and white clover, *Trifolium repens* (23–34%) (Wykes, 1953; Roberts, 1994) and is near the theoretically derived optimal concentration of 55% (Kim *et al.*, 2011). Furthermore, the accessibility of nectar could mean that it is easy to gather and further contribute to the net profitability of foraging on ivy flowers. Ivy nectar, therefore, may be a high quality foraging resource for honey bees and other insects.

Ultimately, however, the importance of ivy to the honey bee should be determined through its effects on fitness, or, in beekeeping terms, colony survival and productivity. For instance, Mattila and Otis (2006) showed experimentally that the pollen collected in spring may have positive effects on brood rearing and honey yield in the ensuing season. McLellan (1976) reported that the colony pollen intake in September is 0–8% of a total intake between June and September, suggesting that it may be helpful for a colony by helping to rear young workers before overwintering. Furthermore, Farrar (1936) [in Keller *et al.* (2005)] found that the colony size in spring (expressed as % of the colony size in autumn) is positively correlated with the amount of pollen stores available to the overwintering colony and that larger colonies grew faster in spring and produced more honey during the first nectar flow period.

In addition to pollen, ivy nectar may also be very important, for example, by improving winter survival, since one of the commonest causes of mortality during this time is starvation due to insufficient food stores in both managed (Steinhauer *et al.*, 2014) and natural colonies, especially those founded in summer by swarms (Seeley, 1978). Moreover, due to wide distribution and abundance of ivy throughout Britain, the foraging

distances may often be short, which would result in foraging profitable enough to make a honey crop, as reported by beekeepers (e.g. Greenway *et al.*, 1975). In line with this, Couvillon *et al.* (2014a) found a twofold reduction in the average foraging distance from July–August to September–October, which can almost certainly be attributed to ivy. Nevertheless, it remains difficult to speculate on the ultimate value of ivy in terms of colony fitness, as further experimental work is needed.

Importance of ivy for other insects

In addition to the honey bee, ivy flowers are visited in abundance by other Hymenoptera, Diptera and some Lepidoptera (Figs. 8.1, 8.3, 8.4). The most numerous species recorded in Falmer in 2011 was the common wasp, *V. vulgaris* (Fig. 8.1b). Workers, males and young queens were all seen. Although ivy attracts a wide range of flower visitors, *Vespula* spp. appear to be by far the most effective pollinators (Ollerton *et al.*, 2007; Jacobs *et al.*, 2010), while Ollerton *et al.* (2007) suggested that ivy is functionally specialised for pollination by *Vespula* spp., as they are likely to exert most selection on flower morphology. Indeed, ivy flowers share a number of traits in common with other wasp-pollinated plants, such as dull, pale green colour and a musky odour (Ollerton *et al.*, 2007). However, in the study of Jacobs *et al.* (2010), the Pollination Potential (PP) index score of wasps (0.90) vastly exceeded that of honey bees (0.02), bumble bees (0.04) and hover flies (0.01) largely due to the difference in their relative abundance (1435 wasps, 57 honey bees, 42 bumble bees and 140 hover flies were recorded). In contrast, this study shows that relative abundance of ivy flower visitors can vary greatly both spatially and temporally. Thus, for example, using the average relative abundance of ivy flower visitors recorded across Sussex in 2012 yields PPI index scores of c. 0.30 for wasps, c. 0.35 for honey bees, c. 0.10 for bumble bees and c. 0.21 for hover flies. Honey bees, bumble bees and hover flies, therefore, are almost certainly important pollinators of ivy.

Other studies have recorded a similar insect fauna of ivy flower visitors consisting of bees (mainly *A. mellifera* and *Bombus* spp.), wasps (*Vespula* spp.), true flies (particularly syrphids) and butterflies, in Hertfordshire, UK (Jacobs *et al.*, 2010), Northamptonshire, UK (Ollerton *et al.*, 2007) and Tuscany, Italy (Vezza *et al.*, 2006). The total number of ivy flower-visiting insect species recorded in Britain is at least 72 from the orders of Dermaptera, Diptera, Hymenoptera and Lepidoptera (Metcalfe, 2005), but the list is certainly not complete. In addition, we recorded the abundance and insect taxa foraging on a suite of garden flowers as part of a different study (Chapter 5: Garbuzov & Ratnieks, 2014a), conducted during July–September 2011 and 2012 near Falmer, UK, and found in total about two times as many bumble bees as honey bees, which is in contrast to this study where honey bees outnumbered bumble bees by about 10 to 1 on ivy. This may suggest that ivy is unattractive to bumble bees. However, it is more likely to reflect the seasonal life cycle of bumble bees with annual colonies, most of which die out by late summer or early autumn (Prŷs-Jones & Corbet, 1991). On average 12.5% of bumble bees had pollen in their baskets, indicating that some colonies were still rearing brood. In contrast, honey bee colonies are perennial and have workers all year round. Common wasp colonies are also annual, but their numbers reach the peak from late summer to early autumn (Edwards, 1980), which may explain why their numbers on ivy were high in 2011. In 2012, however, the common wasp abundance (both relative and absolute) dropped considerably from the previous year, which can be explained by the cyclic population dynamics characterised by extreme variation in yearly abundance known in this species in England (Archer, 1985). Although some *Dolichovespula* wasps are common around the study area (FR pers. obs.), none were seen on ivy, as they have a shorter life cycle with smaller colonies that die out in late summer (Edwards, 1980).

Bumble bees typically forage closer to the nest (450–750 m, Knight *et al.*, 2005) than honey bees, but given the high abundance of ivy on a small scale (Table 8.3), colonies are unlikely to be out of range of ivy in Britain, especially in urban areas where many nests are founded in gardens (Osborne *et al.*, 2008a). Less is known about foraging range in *V. vulgaris*, but in related species *V. rufa* (Arnold (1966) in Spradbery, 1973) and *V.*

pensylvanica (Akre *et al.*, 1975) individuals forage up to c. 900 m away from the nest. The other insects, such as true flies and butterflies, are not central-place foragers, thus may stay in the general vicinity of flowering ivy once it is located.

The ivy bee (*C. hederae*) (Fig. 8.1c) is a solitary bee with a strong preference for ivy floral resources (Bischoff *et al.*, 2005). Müller and Kuhlmann (2008) report that 88% of pollen loads collected by *C. hederae* contain pollen of *Hedera* spp. It is one of the latest bees to emerge in western Europe, with its flight activity beginning in early September and largely coinciding with the ivy flowering period (Kuhlmann *et al.*, 2007). It was first recorded in mainland Britain in 2001 (Cross, 2002) and is rapidly spreading along the south coast (BWARS, 2011). The largest relative abundance of *C. hederae* was recorded in the general location of Seaford, where it comprised 16.5% of all ivy flower visitors (Fig. 8.4; Table 8.2).

On average 91% of butterflies recorded on ivy flowers were red admirals (*V. atalanta*). In autumn adults either enter winter hibernation (Fox & Dennis, 2010) or emigrate southward to breed (Stefanescu, 2001; Brattström *et al.*, 2010). The comma butterfly (*P. c-album*) does not migrate, but does hibernate as an adult, with the second and last generation adults emerging in September (Howarth, 1984). Ivy may be an important source of nectar for improving their survival during these times. The other species seen, the speckled wood (*P. aegeria*), is not a migrant and does not overwinter as an adult but is a woodland specialist. Given that ivy is found in most types of woodland (Metcalfe, 2005), it may be an important food plant for *P. aegeria*. In addition, ivy is a main larval food plant of the holly blue butterfly (*Celastrina argiolus*).

Conclusions

Our results show that ivy flowers have great importance to flower-visiting insects in autumn. Given that ivy is abundant and well-distributed both locally and nationally,

being recorded in almost all 10 × 10 km squares in Britain (Metcalfe, 2005), and because it is doubtlessly the most abundant autumn-flowering species, it is unlikely that there is a more important autumn-flowering plant species in Britain to honey bees and other flower-visiting insects, including late season butterflies. Indeed, ivy may well be a keystone species (Power *et al.*, 1996) for flower-visiting insects in autumn. Our study investigated the value of flowers, but ivy also provides berries and nesting sites for birds (Snow & Snow, 1988; Kurucz *et al.*, 2010) and in Britain alone is a foodplant for 77 species of herbivorous insects and mites (Metcalfe, 2005). In addition, ivy is associated with 47 species of fungus (Metcalfe, 2005). These are almost certainly underestimates. From a human perspective, ivy is rather unappreciated or even considered undesirable, perhaps because its flowers are not showy and because it is a climber. It is frequently blamed for damaging walls and harming trees and so is often removed. But, contrary to popular belief, ivy rarely presents a problem to the trees it climbs (Cowan, 2000). Indeed, it has recently been appreciated for its benefits in the insulation of buildings and pollution reduction in urban areas (Viles *et al.*, 2011). Our study provides further evidence of the benefits of ivy to wildlife, which we hope can be used to inform decisions by householders, land owners, environment managers and policy makers.

Chapter 9

Public approval plus more wildlife: twin benefits of reduced mowing of amenity grass in a suburban public park in Saltdean, UK

Mihail Garbuzov, Katherine A. Fensome, Francis L. W. Ratnieks

Abstract

We examined the effects of reduced mowing on wildflower bloom and flower-visiting insects in the Saltdean Oval, a 6 ha suburban public park in Saltdean, UK. In 2012, a novel management regime was initiated in which approximately half the grass area was left uncut, with the plan being to mow it once per year in autumn. In spring 2013, we set up four blocks, with each block subdivided into four 30 × 5 m strips treated under different mowing regimes: (a) regular mowing every 2 weeks all spring and summer, (b) regular mowing until 2 June, (c) regular mowing until 5 July, and (d) no mowing. The abundance of both flowers and flower-visiting insects increased significantly with reduced mowing, being c. 3 and 5 times greater in (d) than (a), respectively, with (b) and (c) intermediate. Mowing intensity, however, had a weak effect on wildflower species richness, which was only lower in (a). A 1 km bee, butterfly, and moth transect walk, 500 m within the long grass part of the park and 500 m within the short, recorded c. 50× greater insect abundance in the long grass. A questionnaire of public opinion found that 97% of park visitors favoured encouraging insects and wildflowers. In terms of enjoyment of the park, 26% said that it had increased, 64% said that it stayed the same, and 10% said that it decreased. These results present an encouraging example of a potential win–win situation in urban land management change, where the interests of humans and wildlife are aligned, thereby making the goals of conservation easier to achieve.

Introduction

Flower-visiting insects are an important component of insect species diversity and also provide a valuable ecosystem service by pollinating wild plants (Kearns *et al.*, 1998) and agricultural crops (Klein *et al.*, 2007). Pollinators as a guild, however, are in decline globally largely due to human activities, such as intensive land use and the introduction of alien pests and pathogens (Potts *et al.*, 2010a; Vanbergen & the Insect Pollinators Initiative, 2013). Most conservation actions aimed at helping pollinators have been focused on natural (Forup *et al.*, 2008), seminatural (Tarrant *et al.*, 2013), or agricultural landscapes, such as agri-environment schemes that offer subsidies to farmers who adopt wildlife-friendly practices (Batary *et al.*, 2011). Nevertheless the value of urban areas, which can support abundant and diverse communities of flower-visiting insects (Bates *et al.*, 2011; Hennig & Ghazoul, 2012; Matteson *et al.*, 2013) and other wildlife (Angold *et al.*, 2006; McKinney, 2008) is increasingly recognised.

Urban areas encompass large amounts of green space, including parks, gardens, lawns, cemeteries, roundabouts, road verges, railway embankments, and brownfield sites. Domestic gardens alone comprised 22–27% of the urban area in a sample of five large UK cities (Loram *et al.*, 2007), which constitutes an enormous resource for wildlife (Davies *et al.*, 2009; Goddard *et al.*, 2010). Indeed, gardens are often rich in both native and exotic ornamental flowers that provide nectar and pollen for flower-visiting insects (Comba *et al.*, 1999a,b; Matteson *et al.*, 2008; Frankie *et al.*, 2009; Chapter 5: Garbuzov & Ratnieks, 2014a). Road verges can present an important habitat for butterflies and diurnal moths, with the former being attracted by nectar-producing plants and the latter taking shelter in tall vegetation (Saarinen *et al.*, 2005). Urban roundabouts, particularly those of larger area, support abundant and species-rich Hemiptera communities (Helden & Leather, 2004).

Biodiversity in urban green spaces can be further promoted by applying wildlife-friendly management practices. For example, Ahern and Boughton (1994) suggest that wildflower meadows are often sustainable alternatives with ecological, economic, and

aesthetic advantages over the intensively managed turf grass lawns common in the USA. The latter require intensive management in terms of frequent mowing and the input of fertilisers, herbicides, and insecticides. The establishment of a stable community of meadow plants, however, is not a trivial task, as it usually requires the sowing of specifically formulated seed mixes (Bretzel *et al.*, 2012), sometimes supplemented by planting of plants in plugs (Hitchmough, 2000), as well as intensive site and soil preparation, carefully timed annual mowing, as well as control of undesirable 'weeds' (Ahern & Boughton, 1994; Aldrich, 2002). An alternative approach, which is less often considered, is to encourage blooms of existing wildflowers in parks and lawns through reduced mowing. The advantages of this approach include the absence of a need for sowing or planting, as the plant species allowed to flower would be those already present in the community and appropriate for the location.

In this study, we compared the effects of four different mowing regimes on the abundance and richness of wildflowers and the flower-visiting insects attracted in a suburban public park in Saltdean, UK. This park was undergoing a change in management, in which the amenity grass on approximately half of the park was allowed to grow long via reduced mowing. In addition, we surveyed the park users for their opinions on the new management.

Methods

Study site and mowing treatments

The study was carried out in the Saltdean Oval, Saltdean, East Sussex, UK (lat: 50.803341, long: -0.041004538). The Saltdean Oval is a 6 ha public park, mostly amenity grassland, in a suburban area 200 m from the sea coast. The residential district of Saltdean itself is bordered to the north by farmland that is within the South Downs National Park, c. 400 m from the Saltdean Oval at its closest point. The Saltdean Oval is managed by the CityParks

department of the Brighton & Hove City Council. Until recently this involved mowing all the grass every 2 weeks during spring, summer, and early autumn. In 2012–2013, CityParks trialled a novel management regime in an attempt to encourage wildflowers and wildlife. This involved not mowing the eastern half of the park since the autumn (2012), resulting in taller vegetation during the following spring and summer (2013) (Fig. 9.1). The western half was mowed at the normal frequency.

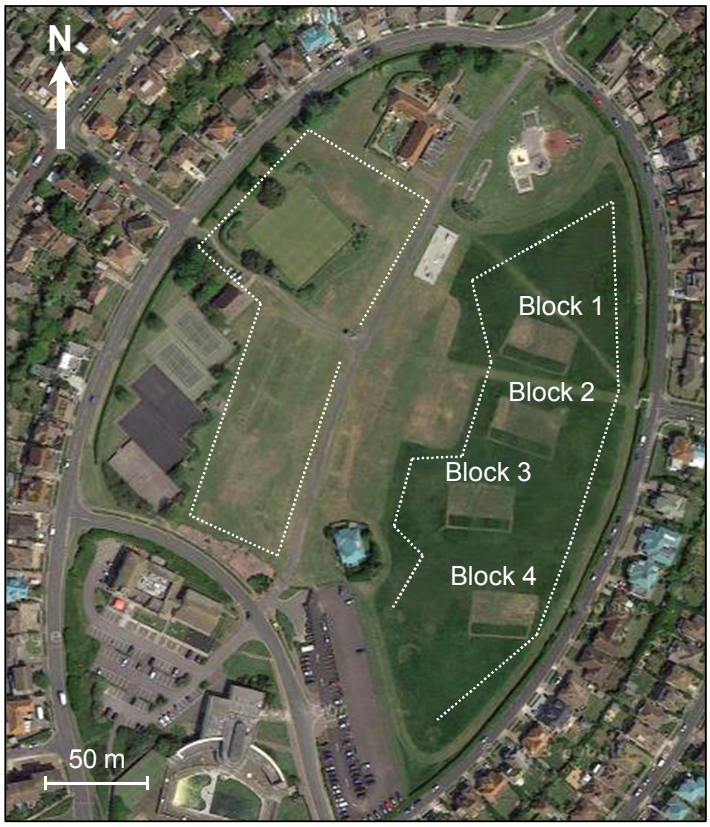


Figure 9.1. Map of the Saltdean Oval park, showing the four experimental blocks on the eastern side. The southernmost strip in each block belongs to the unmown treatment and hence is darker in colour than the other three strips. The two white dotted lines represent the two sections of the transect walk, c. 500 m per section, one in the half of the park that was not mown since the previous year (eastern) and one in the half that was mown regularly (western).

To investigate the effects of different mowing regimes in more detail, four blocks (20 × 30 m) were set out in the eastern half of the park (Fig. 9.1). Each block was subdivided longitudinally into four 5 × 30 m strips, with one strip per block in each of four mowing treatment regimes. The locations of treatment strips within blocks were not randomised. In order of decreasing mowing intensity, these were: (a) regular mowing every 2 weeks (normal management), (b) regular mowing until 5 July 2013, (c) regular mowing until 2 June 2013, and (d) no mowing since the previous year. Thus, treatments (a) and (d) were also representative of the wider areas in the western and eastern park halves, respectively.

Quantifying abundance of flowers and flower-visiting insects

We quantified the abundance of flowers and flower-visiting insects from 18 June to 18 September 2013, a period that included the peak abundance of both (see below in Results). Surveys took place at approximately weekly intervals. Data were collected by one person (KAF), typically over 2 days per week, with flower abundance surveyed on 1 day and insect abundance on the next.

Floral abundance was quantified by surveying the whole area of each strip in each block by eye and counting the number of flowering units of each plant species. In instances when floral abundance was high, the strip was divided into subareas using temporary markers, to reduce the chance of recounting flowering units, as deemed appropriate by the observer (KAF). The number of flowering units was determined by summing the numbers in every patch within a strip, which were counted individually (if ≤20 flowering units) or approximated to the nearest 10 (if >20 flowering units). Flowering unit definition varied among species, and was chosen per species as the smallest unit that could be practically counted (see Appendix 9.1). In some species, this was a single flower (e.g. *Lotus corniculatus*) and in others an inflorescence (e.g. *Trifolium* spp.) (after Carvell *et al.*, 2007). Plant identification and naming followed Streeter *et al.* (2010).

To quantify insect abundance, an observer walked slowly down the centre of each 30-m strip counting all insects on flowers. In each week, each strip was walked five times (5 walks per strip × 4 treatments × 4 blocks). The species of plant each insect was foraging on was recorded. In addition, some insects, predominantly butterflies and moths, were counted as they rested on vegetation. The insects were identified and grouped as follows: Diptera: (i) non-Syrphidae; (ii) Syrphidae (hover flies); bumble bees, *Bombus* spp. (after Fussell & Corbet, 1992); (iii) two-banded white tails; (iv) three-banded white tails; (v) black-bodied red tails; (vi) banded red tails; (vii) browns; (viii) honey bees, *Apis mellifera*; (ix) other bees; Lepidoptera: (x) butterflies and (xi) moths; (xii) Coleoptera; and (xiii) all other insects. Butterflies and two conspicuous diurnal moths, burnets (*Zygaena* spp.) and the silver Y (*Autographa gamma*), were further identified to genus or species.

The insect surveys were conducted between 10:00 and 17:00 BST on days with favourable weather. That is, based on our experience, the insect surveys were made at times when the combination of sunlight, temperature, and wind was such as to allow all insect categories to be active.

In addition, bumble bees, butterflies, and moths were counted in a whole-park transect walk in two sections, each c. 500 m, one in the eastern (long vegetation) and one in the western half (short vegetation) (Fig. 9.1). The transect walk was made eight times at approximately weekly intervals from 7 July to 18 September 2013, and was based on the established methods of the UK Butterfly Monitoring Scheme (http://www.ukbms.org/resources.aspx), and the BeeWalk (http://bumblebeeconservation.org/get-involved/surveys), such that insects, both foraging on flowers and resting, were recorded within 2 m on either side or ahead of an observer walking a defined path.

Survey of public opinion

Opinions of park visitors (n = 39) regarding the different grass mowing regimes were determined using a questionnaire. Park visitors were approached, asked to participate in the survey, and then filled in the questionnaire themselves. Questions were designed to find out their own status (i.e. sex, age, whether resident local or not, frequency of visits, how they use the park etc.), their opinion on the change in grass mowing management and how it affected their use and enjoyment of the park, as well as their desire to learn more about wildflowers and flower-visiting insects and potentially to participate in conservation activities (see full questionnaire in Appendix 9.2). Park visitors were also exposed to the information plaques present around the park with the information about the ongoing experiment and the potential benefits of the reduced mowing to urban wildlife and biodiversity. The survey took place in August 2013 when the differences among the four mowing treatments in the blocks, and also between the western and eastern halves of the whole park, were well developed.

Statistical analyses

To explore the general differences among the four within-block mowing treatments, we fitted three general linear models (GLM), each with either (i) flowering unit density, (ii) species richness of plants per flower, or (iii) mean number of insects on flowers per transect walk in a strip as a response variable, 'treatment' as an explanatory variable, and 'block' as a blocking factor. To account for temporal non-independence of data points taken across the season, AR-1 correlation structure was added to the models (Zuur *et al.*, 2009). The fourth GLM was used to test the relationship between floral abundance and insect abundance using the number of insects on flowers per transect walk in a strip as a response variable, flowering unit density as an explanatory variable, and 'block' as a blocking factor. Models were fitted in R v.3.0.2 (R Core Team, 2013) using function *gls* (package *nlme*, Pinheiro *et al.*, 2013). Associations between key questionnaire responses and respondent status were tested using the chi-squared test.

Results

General differences among the four mowing treatments

Each of the three measures: (i) flowering unit density, (ii) species richness of plants in flower, and (iii) number of flower-visiting insects per transect walk in a strip, differed significantly among the mowing treatments (Table 9.1). Tukey's *post-hoc* tests showed an increasing trend in each response variable with a reduction in mowing intensity (Table 9.1). For instance, flowering unit density was approximately three times higher in the unmown treatment (16.9 ± 1.8 flowering units per m^2) compared to regular mowing (5.5 ± 0.7 flowering units per m^2), and the mean number of insects on flowers per transect walk was five times higher (7.0 ± 1.1 *vs.* 1.4 ± 0.2). Yet, the number of plant species in flower reached a plateau at an intermediate mowing intensity (range of means 11.7–12.8

species per strip), only slightly higher than with regular mowing (9.2 ± 0.5 species per strip).

Table 9.1. Effects of mowing treatment on the number of plant species in flower, flowering unit density, and the number of flower-visiting insects

			Treatment estimates[a]			
	F-value	P-value	Regular mowing	Mowing until July	Mowing until June	No mowing
Number of flowering units per m^2						
Mowing treatment	5.13	0.002	5.5±0.7 (a)	8.8±0.8 (ab)	9.7±0.9 (b)	16.9±1.8 (c)
Block	15.62	<0.001				
Number of plant species in flower per strip						
Mowing treatment	5.16	0.002	9.2±0.5 (a)	11.7±0.6 (b)	12.1±0.5 (b)	12.8±0.4 (b)
Block	18.39	<0.001				
Mean number of insects on flowers per transect-walk in a strip						
Mowing treatment	4.40	0.005	1.4±0.2 (a)	3.1±0.5 (ab)	4.6±0.6 (b)	7.0±1.1 (c)
Block	5.87	0.001				

[a]Means ± standard errors of treatment estimates. Lowercase letters in brackets indicate homogeneous subsets based on Tukey's post-hoc tests (Appendix 9.3), where treatments sharing a letter are not significantly different at α=0.05

In the unmown treatment, the 10 plant species with the highest numbers of flowering units accounted for 84% of all flowering units recorded over the monitoring period. The same 10 species also comprised the majority (85–89%) of flowering units in other three treatments, showing similarity in plant species composition (Fig. 9.2; Appendix 9.1).

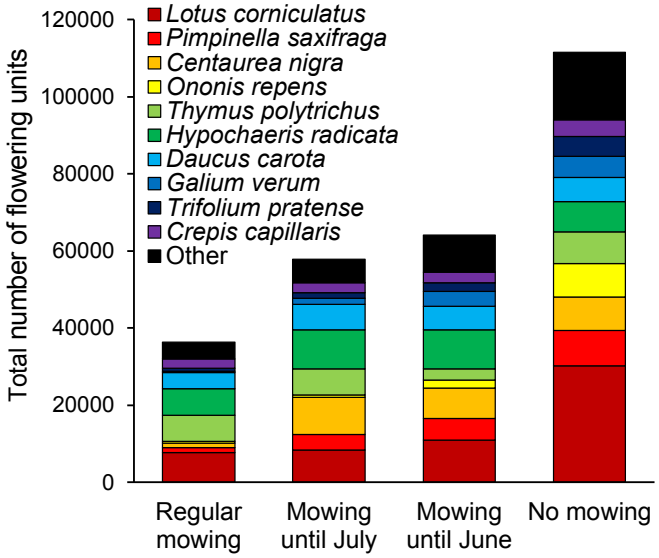


Figure 9.2. Relative abundance of flowering units recorded in the four mowing treatments over the whole study period, 18 June–18 September 2013. The ten named species comprised 84–89% of all flowering units in each treatment.

Floral abundance as driver of insect visitation

Although our data cannot be used to show a causal link between the abundance of flowers and flower-visiting insects, as floral abundance was not directly manipulated experimentally, such a link can be inferred correlatively. Indeed, flowering unit density was a significant predictor for the mean number of insects on flowers per transect walk in a strip ($F_{1,171} = 17.57$, $P < 0.001$; block: $F_{3,171} = 2.46$, $P = 0.065$). This can also be seen in the temporal trends of both these variables, as they tend to covary within and among treatments (Fig. 9.3).

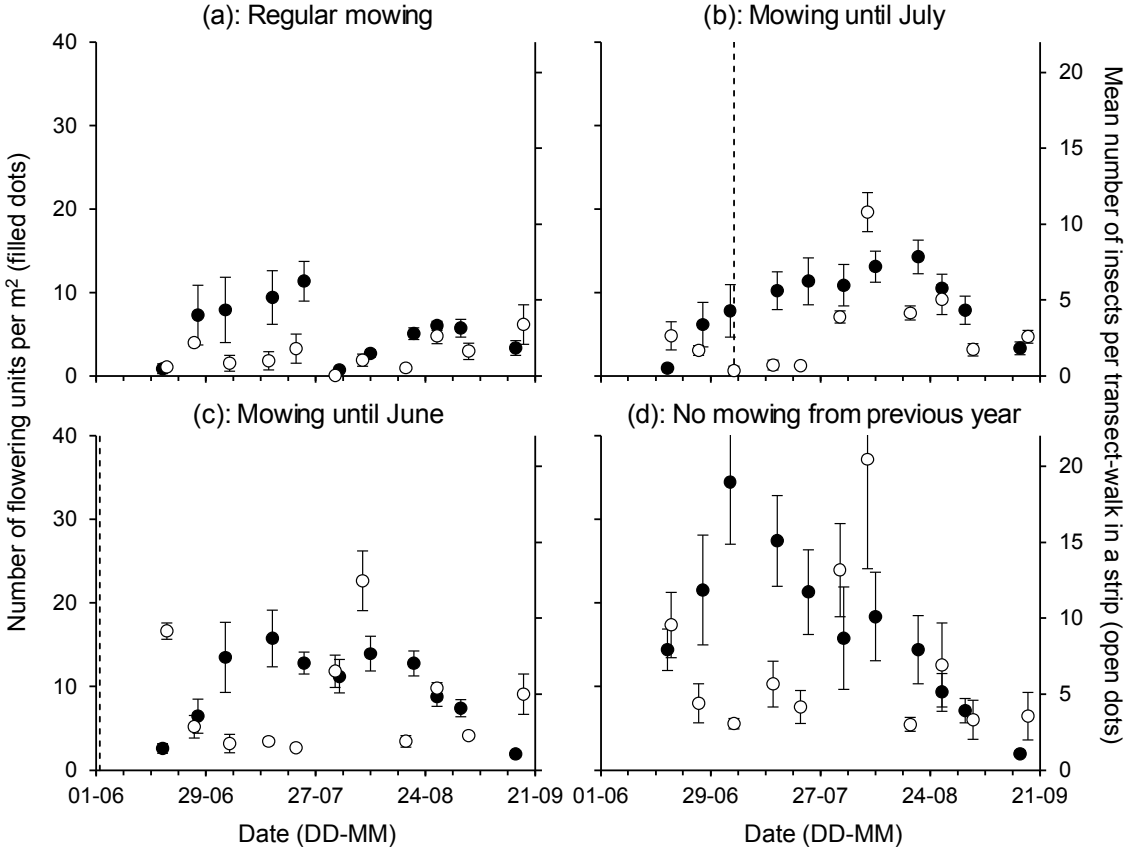


Figure 9.3. Temporal variation in flowering unit density (●, filled dots) and abundance of flower-visiting insects (○, open dots) in the four mowing treatments over the monitoring period from 18 June to 18 September 2013. Vertical dashed lines indicate the last mowing date: 5 July in (b) and 2 June in (c). Dots are means per block ± standard error.

Across the monitoring period, the most numerous insects seen visiting flowers were flies (47.8%), of which 10.8% were syrphids and 89.2% non-syrphids, and bumble bees (35.0%), of which 12.1% were two-banded white tails, 1.0% three-banded white tails,

19.1% banded red tails, 60.1% black-bodied red tails, and 7.8% browns. Honey bees comprised only 0.1% of all insects and other bees 1.9%. Lepidoptera were 6.9%, of which about half were butterflies (54.3%) and half were moths (45.7%). Coleoptera were 7.3% and all other insects 0.8%. Further breakdowns of butterflies and moths into relative abundances of individual species are given in Table 9.2. The two most numerous butterfly species were the common blue, *Polyommatus icarus*, and meadow brown, *Maniola jurtina*. Nearly all moths recorded visiting flowers were diurnal species: Silver Y, *Autographa gamma*, and burnets, *Zygaena* spp. In contrast, the majority of moths recorded while resting were other, presumably largely nocturnal, species.

Table 9.2. Abundance of butterflies and moths on flowers or resting in vegetation recorded in the experimental blocks

		Visiting flowers		Resting	
Butterflies		%[a]	Count	%[a]	Count
Lycaenidae					
Lycaena phlaeas	Small copper	<1%	1	-	-
Polyommatus icarus	Common blue	59%	78	56%	60
Nymphalidae					
Maniola jurtina	Meadow brown	30%	39	39%	42
Pyronia tithonus	Gatekeeper	2%	2	-	-
Pieridae					
Pieris brassicae	Large white	3%	4	-	-
Pieris rapae	Small white	5%	7	2%	2
Hesperiidae					
Ochlodes sylvanus	Large skipper	-	-	1%	1
Thymelicus sylvestris	Small skipper	<1%	1	2%	2
Moths					
Autographa gamma	Silver Y	58%	64	1%	4
Zygaena spp.	Burnet moths	34%	38	2%	5
Unidentified		8%	9	97%	322

[a]Relative abundance among either butterflies or moths, respectively

Figure 9.4 presents the total numbers of insects recorded visiting flowers of 24 plant species or resting in the vegetation, in the four treatments. These total numbers are likely to be affected by several factors, including the abundance of flowers, length of flowering period, and the intrinsic attractiveness per flower, and therefore represent a measure of the overall importance of each plant species in each treatment. Eighteen plant species recorded flowering were not seen being visited by a single insect.

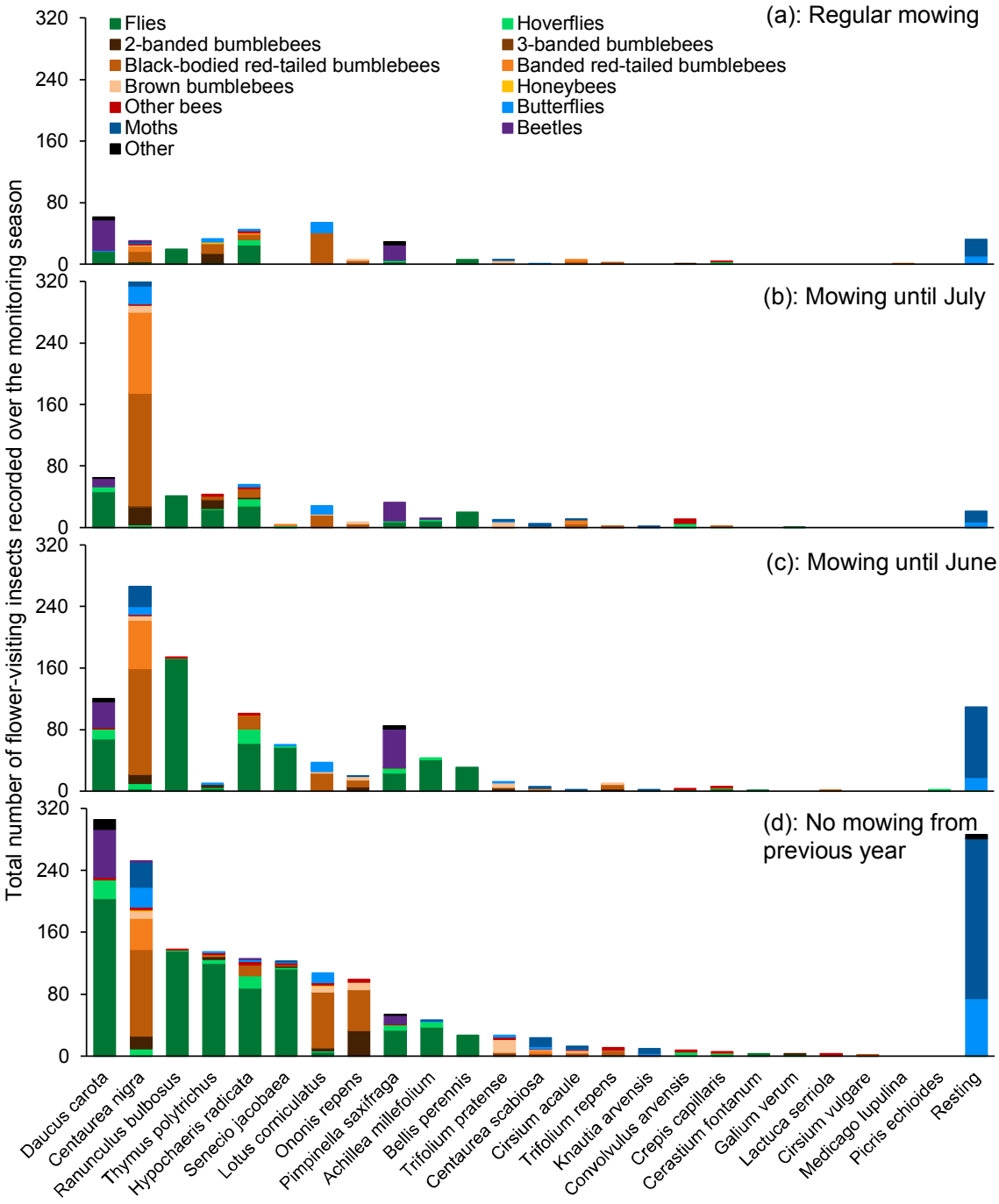


Figure 9.4. Total numbers of insects counted over the whole project period (18 June–18 September 2013) visiting the flowers or resting in the four mowing treatments. Panels are arranged in order of decreasing mowing intensity from top to bottom. The bars represent the 24 plant species that received insect visits, arranged in descending order of insect attractiveness in the most attractive treatment (d). For taxonomic definitions of insect groups see Methods. An additional 18 flower species received zero insect visits and are not shown (see Appendix 9.1).

Whole-park transect walks

The abundance of bumble bees, butterflies, and moths recorded in the whole-park transect walks was similarly affected by mowing to that recorded in the blocks, but showed an even greater difference between the area that was not mown since the previous year (eastern half) and the area that was mown regularly (western half), with c. 50-fold greater insect abundance in the former (Fig. 9.5). A comparable data subset from the blocks, excluding all insect categories except bumble bees, butterflies, and moths, but including resting individuals, showed 4.7 times greater abundance of insects in the unmown treatment (d) than in the regularly mown treatment (a) [totals: (d): 120 bumble bees, 32 butterflies, 23 moths *vs.* (a): 433 bumble bees, 123 butterflies, 261 moths]. The greater difference between these two treatments in whole-park transect walks compared to the shorter transect walks within the blocks is probably attributable to the lesser wildflower density in the former, although this was not quantified and was only noted casually. In addition, it is possible that the insect abundance in the regularly mown strips benefitted from closer proximity to the unmown vegetation.

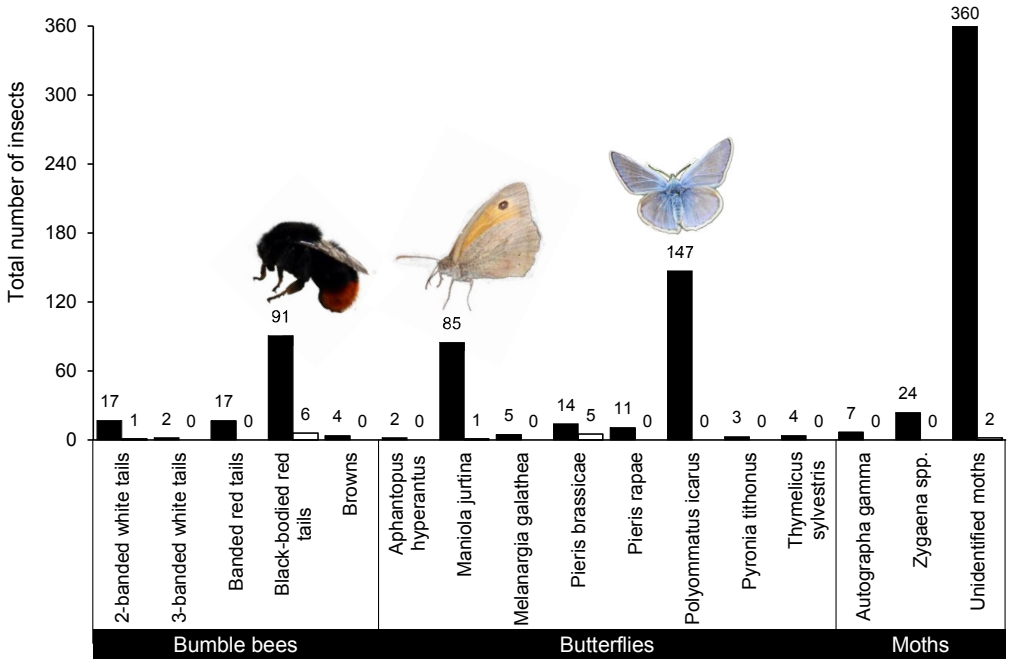


Figure 9.4. Total abundance of bumble bees, butterflies, and moths recorded in the two 500 m sections of the whole-park transect walk (Fig. 9.1) repeated over the monitoring period (for dates see Methods): the eastern half of the park had not been mown since the previous year (filled bars) and the western half that was mown regularly (open bars). The numbers for each insect group are shown above the bars. The total number of insects recorded was 793 (98.1%) (unmown) and 15 (1.9%) (mown regularly). The three commonest types of insect recorded in the area of tall vegetation, apart from unidentified moths, were black-bodied red-tailed bumble bees (illustrated by *Bombus lapidarius*), meadow brown butterflies (*Maniola jurtina*), and common blue butterflies (*Polyommatus icarus*).

Opinions of park visitors

The 39 park visitors were 69% females and 31% males. Most were local residents (86%), who visited the Saltdean Oval once per week or more often (80%). Sixty per cent visited almost every day. Most respondents (74%) felt that the amount of unmown taller vegetation in the park was appropriate and had not caused them to change their normal way of use of the park (77%). The minority, 23%, who were affected negatively in use of the park gave reasons, such as 'avoidance of the long grass areas' and 'extra care needed to be taken when walking the dog'. Correspondingly, most respondents, 64%, did not feel that the unmown area changed how much they enjoy the park, while 26% enjoyed it more due to more colour brought in by wildflowers and butterflies and only 10% enjoyed it less.

Ninety-seven per cent agreed with the statement that 'it is a good idea to encourage bees and butterflies'. Although 54% wanted to learn more about wildlife, only 38% indicated that they would be interested in helping to collect data about these species in the park. For the full questionnaire and summary of all responses, see Appendix 9.2.

We did not detect any associations between resident status (sex, age group, local residency or frequency of visits to the park) with responses to the key questions regarding the opinion or effect of a change in grass management (Table 9.3), although the tests need to be interpreted cautiously due to the small sample size.

Table 9.3. Twelve χ^2 tests of association between respondent status and opinions/effects of a change in grass management. No P-value was lower than the α-level corrected for 12 tests using the Bonferroni method (0.05 / 12 = 0.004).

	Is the amount of long grass appropriate?		Has the long grass changed how you use the park?		Has the long grass changed how much you enjoy the park?	
Sex	Yes	No	Yes	No	Yes	No
Male	6	3	2	7	4	5
Female	15	5	5	15	6	14
χ^2 (d.f.)	0.216 (1)		0.026 (1)		0.573 (1)	
P-value	0.642		0.872		0.449	
Age group						
18-30	1	1	1	1	0	2
31-40	9	0	1	8	2	7
41-50	1	4	3	2	2	3
51-60	4	0	0	4	1	3
61-70	5	2	3	4	3	4
70+	7	3	1	9	5	5
χ^2 (d.f.)	12.517 (5)		8.734 (5)		3.127 (5)	
P-value	0.028		0.120		0.680	
Living locally						
Yes	24	8	6	26	12	20
No	4	1	2	3	1	4
χ^2 (d.f.)	0.059 (1)		1.152 (1)		0.581 (1)	
P-value	0.809		0.283		0.446	
Frequency of visits						
Rarely	3	1	2	2	1	3
Less than once a month	2	1	0	3	1	2
Once a week	5	2	0	7	2	5
Almost every day	16	5	6	15	9	12
χ^2 (d.f.)	0.162 (3)		5.023 (3)		0.785 (3)	
P-value	0.983		0.170		0.853	

*Note some observed cell counts are <5, so the test results need to be interpreted with caution.

**Some participants did not provide answers to all questions and were excluded from respective tests.

Discussion

Although our study was conducted in a single park, the results clearly show that a reduction in mowing intensity may increase the abundance of wildflowers and the insects that visit these flowers in the urban green space being managed. Mowing, however, had relatively little effect on flower species richness, which was only slightly lower in the treatment that was mown regularly, compared to other treatments, indicating that the species pool of flowers was similar in every treatment (Appendix 9.1). Data collection in

this study ceased on 18th September, when most plants had finished or nearly finished flowering (Fig. 9.3). But any plants that do flower later into autumn may be of particular importance to flower-visiting insects, given that there are few wildflowers in bloom at this time of year in the study area (Chapter 8: Garbuzov & Ratnieks, 2014b) and probably generally in Britain. We have previously shown that, in autumn (mid-September to mid-October), an average of 89% of pollen collected by the generalist forager, the honey bee, *A. mellifera*, comes from ivy, *Hedera helix* and/or *Hedera hibernica*, indicating that there are very few other plants still in flower (Chapter 8: Garbuzov & Ratnieks, 2014b).

Mowing and other lawn management practices are known to affect floral diversity and composition (Bertoncini *et al.*, 2012). Nevertheless the Saltdean Oval has been mown regularly for many years, so the grassland community was probably filtered for species tolerant to mowing. Following a change in mowing intensity, it would probably take more than 1 year (the duration in this study) for differences to develop. Similarly, Thompson *et al.* (2004) failed to detect any effects of variation in ongoing mowing frequency, ranging from twice per week to once per month, on plant diversity in lawns in a sample of 52 domestic gardens in Sheffield, UK.

Our results have parallels to projects from other countries. For example, in Paris, France, public gardens can receive 'biodiversity-friendly' certification based on the extent to which they employ recommended 'differential management' practices, which include a reduction in lawn mowing frequency, but also water saving, composting, and a reduction in the use of pesticides (Shwartz *et al.*, 2013). Gardens certified in this way support a higher diversity of plants, birds, pollinators in general (and butterflies in particular), with a strong positive correlation between the richness of plants and that of pollinators (Shwartz *et al.*, 2013).

Noordijk *et al.* (2009) studied the effects of mowing roadside verges in the Netherlands. Mowing twice a year (the highest mowing frequency studied) versus once or not mowing, generally resulted in higher floral abundance and diversity, as well as abundance of flower-visiting insects and the number of visits to flowers, showing that some disturbance can be beneficial. These effects were attributed to the re-flowering of

some plants later in the season after the early summer mow (in addition to the mow in early autumn), which resulted in greater overall availability of flowers across the season. Furthermore, mowing frequencies as low as once or twice per year can, in principle, have a positive effect on floral abundance and diversity by reducing competitive dominance of grasses in favour of forbs (Bobbink & Willems, 1993; Williams *et al.*, 2007). In contrast, our results showed a decrease in floral and insect abundance with increasing mowing intensity compared to the unmown control. This is probably because all mown treatments were mown at a high, 2-week, frequency for a lengthy period of time, which is considerably more intensive than the annual or biannual mowing typical in meadow management. Similarly, Valtonen *et al.* (2006) found a positive effect of reduced mowing intensity on the abundance and richness of diurnal Lepidoptera in roadside verges in Finland. Reduced mowing intensity was achieved either by delaying the annual mow until late summer, or by mowing only a part of the road verge area, resulting in a mosaic habitat structure.

Giuliano *et al.* (2004) showed that urban parks of the New York City, USA, can be an important habitat for Lepidoptera, where herbaceous vegetation is used both for nectaring and resting. Indeed, in addition to increased floral resources, reduced mowing can improve the habitat for butterflies and moths by allowing vegetation height to increase, thus providing shelter and resting sites. Shelter is an important factor affecting butterfly population sizes by having an effect on the microclimate of the larval habitat, affecting the propensity of adults to disperse between habitat patches and providing refuge at night or during inclement weather (Thomas *et al.*, 2011). In our study, however, considerable numbers of resting Lepidoptera were recorded only in the unmown treatment, which had the tallest vegetation, and moderate numbers in the next least intensively mowed treatment, which was mowed until early July. Similarly, Saarinen *et al.* (2005) found that the availability of tall vegetation was the main factor related to high numbers of diurnal moths recorded in road verges in Finland.

The results of the public opinion survey are encouraging as they show that a change in park management that benefits wildlife is generally met with approval. This

parallels the experience from The Hague, Netherlands, where citizens are actively involved in planning, decision-making, and data collection pertaining to the management of urban green spaces, with a positive effect on the maintenance of urban biodiversity (Mabelis & Maksymiuk, 2009). Similarly, a telephone survey in Cleveland, USA, found that over half of the interviewees believed that park land should be primarily used for conservation (56%) rather than recreation (44%), and the majority indicated a preference for nature-based recreation (63%), as opposed to organised fitness activities (37%) (Payne *et al.*, 2002). In our survey, almost all respondents, 97%, favoured encouraging wildflowers and insects, and most, 74%, approved the long grass in the Saltdean Oval. Indeed, nature in urban green spaces may have a positive influence on human psychological well-being, such as by eliciting positive feelings and emotions that fulfil nonmaterial needs (Chiesura, 2004). Fuller *et al.* (2007) have shown that these psychological benefits increase with greater biodiversity. A recent nationwide UK survey found that people living in urban areas with more green space are happier, have greater life satisfaction and lower levels of mental distress (White *et al.*, 2013). Although these psychological benefits might be seen as a by-product of promoting green spaces and encouraging wildlife in urban areas, Dearborn and Kark (2010) argued that they may, in turn, catalyse greater public support for biodiversity conservation in general. About a quarter of park visitors in our survey, however, expressed discontent with the areas of tall grass, particularly dog walkers, who commented that plant seeds and other dirt can easily get entangled in dog fur. Dog walkers are also required to pick up and dispose of their dog's faeces, which is probably more difficult to do in the tall grass (c. 40 cm), compared to the short, regularly mown, grass (c. 5 cm). In addition, some people may feel that long grass is untidy as they are used to urban and suburban parks with short grass, which is traditional in the UK.

Overall, our results show that the change in vegetation management trialled in the Saltdean Oval appears to be beneficial from the perspectives of both biodiversity conservation and public attitude. In principle, reduced mowing also reduces costs, although with annual mowing the savings are offset by the cost of disposing of the cut

vegetation in an approved way (M. Thomas & M. Gapper of CityParks, Brighton & Hove City Council, pers. comm.). In contrast, there is no disposal cost with regular mowing, as the cuttings are simply left in place to decompose. In the conflict between the needs of biodiversity conservation and human land use, such as agriculture or urban development, the latter has taken unquestionable priority in the past (Robinson & Sutherland, 2002; McDonald *et al.*, 2008). Nonetheless, conserving biodiversity is an important part of sustainability (Hooper *et al.*, 2005). Our results from the Saltdean Oval present an example of a win–win situation in land management change, where the interests of humans and wildlife are aligned, thereby making the goals of conservation easier to achieve (Hutton & Leader-Williams, 2003).

Research Chapters

Part 4: Using Waggle Dance Decoding to Investigate Foraging by Urban Honey Bee Colonies

Photo credit: Cristoph Grüter

Chapter 10

Eating locally: dance decoding demonstrates that urban honey bees in Brighton, UK, forage mainly in the surrounding urban area

Mihail Garbuzov, Roger Schürch, Francis L. W. Ratnieks

Abstract

Urbanization is increasing worldwide. Urban habitats often support considerable biodiversity and so are of conservation value, even though they are highly modified ecosystems. Urban parks and gardens are rich in flowers that provide food for pollinators, including bees. Here, we use waggle dance decoding to investigate foraging by 3 honey bee hives located in the city of Brighton, UK, over almost an entire foraging season, April to October. Waggle dances were recorded using video cameras and decoded during framewise playback on a computer by measuring the angle and duration of the waggle phase. Foraging was mostly local (mean monthly distances 0.5–1.2 km) and mostly within the surrounding urban area (monthly means 78–92 %) versus the countryside (closest distance 2.2 km) even though this was well within the honey bee maximum foraging range (c. 12 km). These distances were lower than those from a previous study for hives located in a rural area 4.5 km away. Honey bees are very sensitive to foraging economics and foragers make waggle dances only after visiting high-quality feeding locations. Low distances advertised by dances, therefore, indicate sufficient forage nearby and show that urban areas can support honey bees year round. As a corollary, however, urban bees may provide little pollination service to agriculture especially in spring, which had the lowest foraging distances and is when the most economically important animal-pollinated UK crops, apple and oilseed rape, are in bloom.

Introduction

Urban and suburban areas cover 0.4%of the ice-free land area worldwide (Ellis *et al.*, 2010), but more in the UK (6.8–9.5 %, depending on definition; UK National Ecosystem Assessment, 2011). More than half (51 %) of the world's population now lives in urban, rather than rural areas, and this is projected to increase to 68 % by 2050 (United Nations, 2012). Urban habitats are highly modified and are generally inferior to natural or semi-natural ones for most types of wildlife (McKinney, 2008). Nevertheless, urban areas can support considerable biodiversity (Angold *et al.*, 2006; Davies *et al.*, 2009; Bates *et al.*, 2011) and are of current interest in conservation (Dearborn & Kark, 2010; Sanderson & Huron, 2011) and the emerging field of urban ecology (Gaston, 2010; Niemelä, 2011).

Urban gardens, parks and other green spaces contain flowers which can provide food for pollinators, such as bees, butterflies and hover flies (Kadlec *et al.*, 2008; Goddard *et al.*, 2010; Matteson & Langellotto, 2010; Hennig & Ghazoul, 2012). In some urban areas beekeepers can make good honey crops (Burgett *et al.*, 1978). In the UK, urban beekeeping is increasingly popular, with the number of managed colonies in London tripling to over 3,500 during the past 5 years (Alton & Ratnieks, 2013).

Honey bee foragers use the waggle dance to communicate the locations of food sources to their nestmates (von Frisch, 1967). Each dance provides a vector (direction and distance) from the nest to the dancer's foraging location (Riley *et al.*, 2005). Since bees only dance to advertise the most profitable food sources, the dances present filtered information about the most profitable foraging locations known to a colony at that time (Seeley, 1994; 2012). By decoding many dances, it is possible to build up a picture of where a colony or a group of colonies is foraging and how this changes with time. Thus, waggle dance decoding is a powerful and unique methodology for studying honey bee foraging.

Most previous studies using dance decoding to investigate honey bee foraging focused on agricultural or natural landscapes and typically restricted their data collection to just a few months of a longer foraging season (e.g. Visscher & Seeley, 1982; Steffan-Dewenter & Kuhn, 2003). Here, we decoded dances from 3 urban hives over most of an

entire foraging season, April to October, to explore urban foraging and for comparison with similarly collected data from hives located 4.5 km away in a rural location (Couvillon *et al.*, 2014a).

Methods

Study location and honey bee colonies

We studied three honey bee colonies housed in glass-walled observation hives located at an environmental studies building of a local school with a special interest in conservation (Dorothy Stringer School, latitude: 50.849370, longitude: −0.14167996) in Brighton, UK, a city that is part of a conurbation of 474,000 residents (Office for National Statistics, 2011). The school is in the north-central part of the urban area, c. 2.2 km from countryside (see Fig. 10.3).

Each hive had three medium and one deep Langstroth frames, an egg-laying queen, brood of all ages, and c. 2,000–5,000 workers. Worker bees and brood were removed as necessary to prevent swarming, which is triggered by overcrowding. To prevent possible starvation, colonies were fed 500 ml of 2 M sugar solution most weeks after videoing for data collection (see below), so that the syrup had been consumed several days before data collection resumed.

Waggle dance analysis

Colonies were monitored from 20 April to 16 October in 2011, which encompasses most of the foraging season (March/April–October/November) in the UK. The dance area of each hive was video-recorded, 25 frames per second, for 1 h at approximately weekly intervals using video cameras (Canon Legria HV40) between 10:00 and 16:00 BST during favourable foraging weather (>15 °C, no strong wind, no rain). Individual dances were

analysed by framewise playback on an iMac computer using MPEG Streamclip v.1.9.2 freeware. Up to 20 waggle dances per hour were analysed following the methods of (Couvillon *et al.*, 2012), where four middle, consecutive waggle runs per dance are decoded to obtain mean duration, which encodes distance, and mean angle, which encodes direction.

Distance was estimated using a Bayesian linear calibration model built for our honey bee population in the nearby landscape (Schürch *et al.*, 2013), which takes into account the imprecision inherent in the honey bee dance (Couvillon, 2012). Probability distributions for both vector component estimates (distance and direction) were obtained by simulating each decoded dance 1,000 times, which enabled us to map the foraging locations shown by the dances in a manner that includes the uncertainty in the dance vector (Schürch *et al.*, 2013). This methodology also allowed us to determine confidence intervals for our estimates of the proportion of foraging in urban versus rural areas. The definition of urban areas followed the Ordnance Survey maps for GIS (vector 'Meridian 2') provided by Digimap service (EDINA, http://digimap.edina.ac.uk).

All statistical analyses were performed in R. v.3.0.2 (R Core Team, 2013). The effects of month as a fixed factor on the responses of the average foraging distance and the proportion of urban foraging were analysed using General Linear Mixed Models (GLMM, function *lme*, package *nlme*, Pinheiro *et al.* 2013), as described by Zuur *et al.* (2009), with 'colony' included as a random factor to account for any non-independence of data within colonies. The proportions of urban foraging associated with each waggle dance were estimated by averaging over 1,000 simulations (see above), thus yielding one independent proportion estimate per dance. These estimates were arcsine square root transformed prior to analyses. Months were compared pairwise using *post-hoc* Tukey's HSD test (function *glht*, package *multcomp*, Hothorn *et al.* 2008). All values reported are means±95 % confidence interval.

Results

Foraging distance

Mean estimated foraging distances ranged from 461 m in May to 1,229 m in July (Table 10.1), differing significantly among months (L=124.09, df=6, P<0.001). The addition of colony as a random factor did not significantly improve the fit of the model (L=2.96, df=1, P=0.085), indicating that there were no strong differences among colonies (Fig. 10.1). The results of Tukey's *post-hoc* pairwise comparison test are shown in Fig. 10.2a. Average distance was under 1 km throughout the season, with the exception of July, when it peaked at 1,229 m (Table 10.1, Fig. 10.2a). There was also a slight increase in estimated foraging distance in October (Table 10.1, Fig. 10.2a). This pattern can also be seen in the distribution maps (Fig. 10.3).

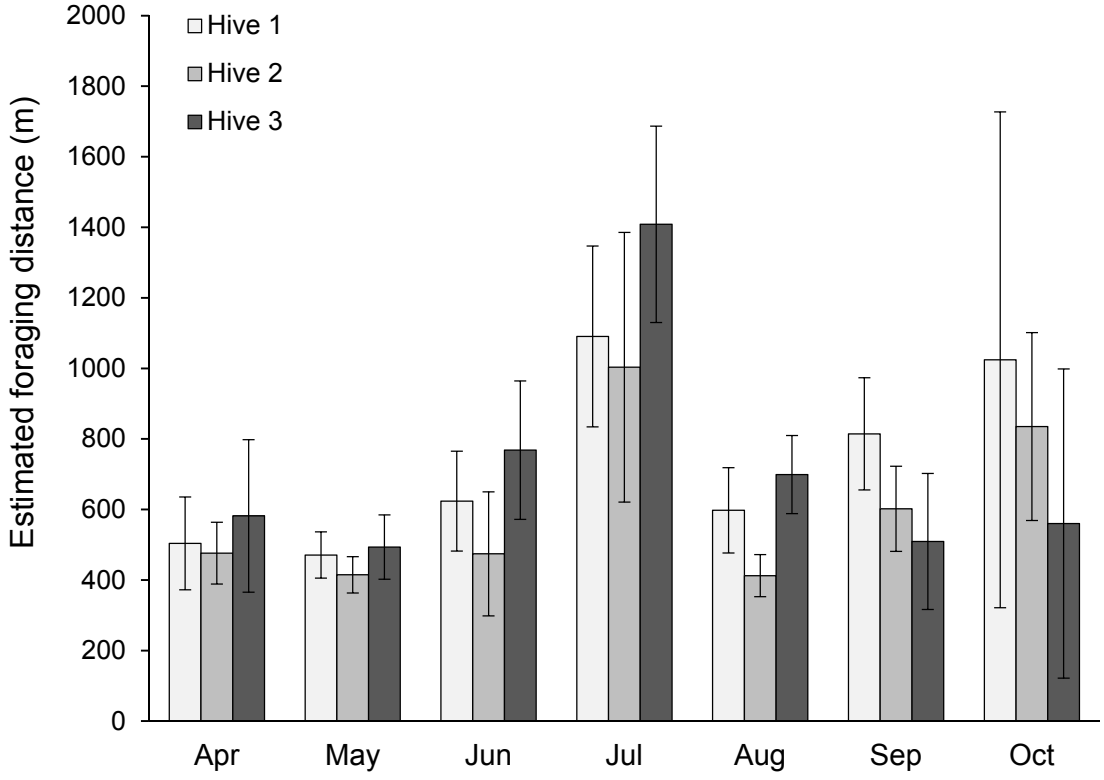


Figure 10.1. Seasonal variation in estimated foraging distance in each of three honey bee hives, as determined by waggle dance decoding (bar heights are means±95 % CI)

Table 10.1. Seasonal variation in honey bee foraging patterns in an urban environment

Month	Foraging distance (m)		Proportion of foraging in urban areas			Number of waggle dances
	Mean	95% CI	%[a]	95% CI[b] lower	95% CI[b] upper	
April	518	86	91.8%	82.6%	96.0%	61
May	461	41	87.0%	82.2%	90.7%	234
June	670	110	87.0%	79.8%	91.9%	116
July	1229	175	79.9%	73.9%	84.7%	209
August	589	64	83.1%	76.7%	87.9%	166
September	685	96	87.1%	79.0%	92.2%	95
October	846	235	77.8%	64.7%	86.9%	50

[a]Percentage among simulated locations

[b]Agresti-Coull 95% confidence intervals, where *p* (number of simulated locations in urban areas) and *n* (total number of simulated locations) are scaled back to the number of waggle dances decoded

Proportion of foraging in urban areas

As the colonies were located 2.2 km from the nearest rural border, foraging at mean distances less than 1.2 km meant that most was in the urban area (78–92 %; Table 10.1, Figs. 2b, 3). Differences among months were significant (L=32.38, df=6, P<0.001), but not among colonies (L<0.001, df=1, P=0.999). Tukey's *post-hoc* pairwise comparison test showed no clear linear pattern across time. As expected, the results followed mean foraging distance, with lower proportions of urban foraging in months when the foraging distances were greatest (e.g. July, October) and *vice versa* in months when mean foraging distances were short. The negative correlation, however, was not significant, although borderline (Pearson's r=−0.71, P=0.074, n=7).

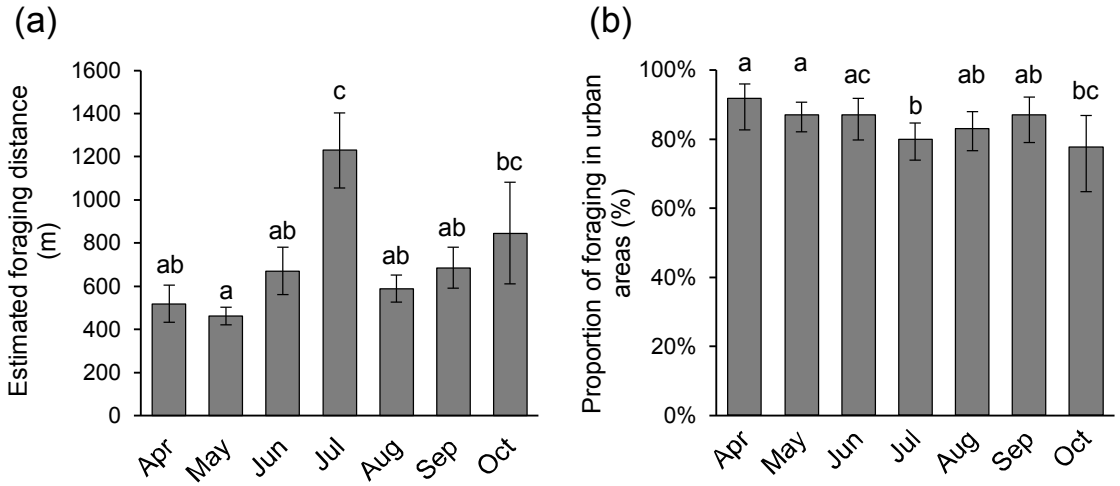


Figure 10.2. (a) Seasonal variation in estimated a honey bee foraging distance, as determined by waggle dance decoding (bar heights are means±95 % CI) and (b) proportion of foraging in the urban areas (bar heights are proportions±95% Agresti-Coull CI, which are not symmetrical around the proportion; Brown *et al*. 2001)

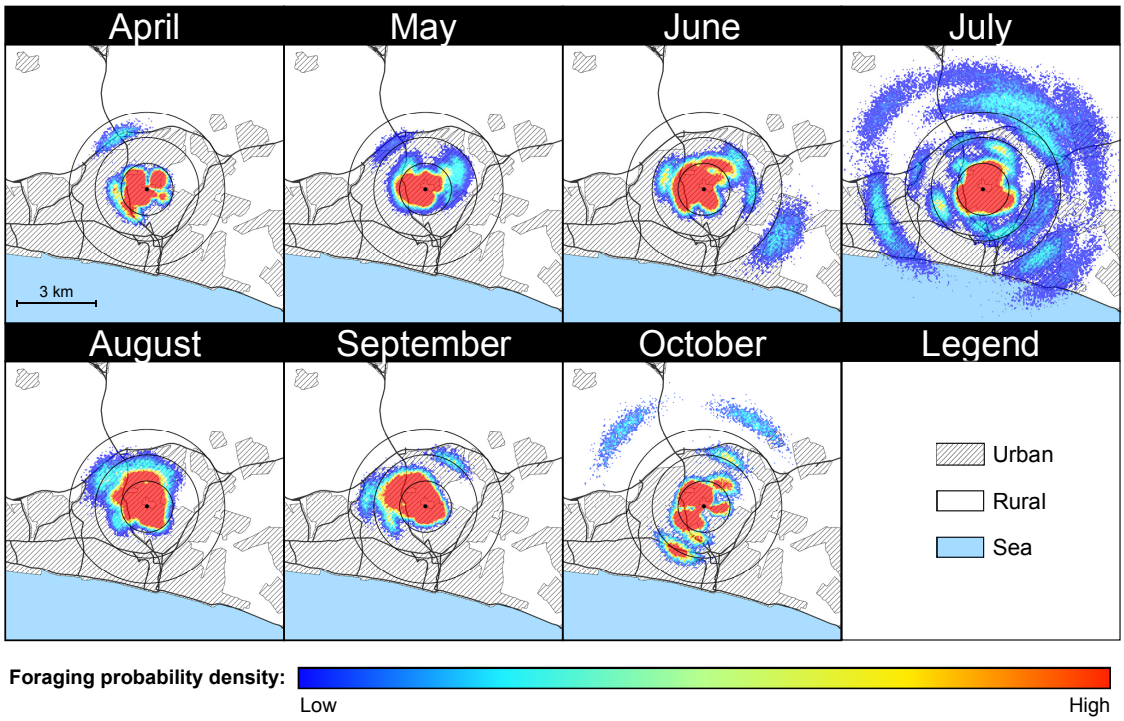


Figure 10.3. Seasonal variation in probability density distributions of urban honey bee foraging from April to October 2011, as determined by waggle dance decoding. Circles, radius 1, 2, 3 km, are centred on the location of the 3 study hives at the Dorothy Stringer School, Brighton, UK. Colour spectra show the range of relative foraging probabilities, as determined by simulated waggle dance locations, binned into 25×25 m quadrats, from blue (1) to red (632–3272, depending on month)

Discussion

Our results clearly show that most foraging from the urban colonies was at relatively short distances (monthly means 0.5–1.2 km) and thus within the surrounding urban area year round (78–92 %), even though the countryside was well within honey bee foraging range (Ratnieks, 2007). In contrast, colonies at the neighbouring rural location (4.5 km distant on the University of Sussex campus) had higher foraging distances except in April and May, when distances were low and comparable with our data, indicating abundant high-quality forage within short distances of both apiaries (Couvillon *et al.*, 2014a). In the urban colonies, the mean foraging distance had no clear pattern across time and showed a single-month peak in July (1.2 km), while in the rural hives distances increased from spring (March–May, 0.5–1.0 km) to late summer (July – August, 1.5–2.5 km) and then declined in autumn (September – October, 0.7–1.5 km) (Couvillon *et al.*, 2014a).

Beekman and Ratnieks (2000) showed that bees located in the city of Sheffield, UK, will travel many kilometres (mean 5.5 km) to forage in the countryside in August. At this time and in this area the countryside provides exceptional foraging opportunities. It is the peak bloom time of heather (*Calluna vulgaris*), which covers many square kilometres of the moors in the Peak District to the west of Sheffield. Heather is a major UK honey crop (Crane, 1976), with beekeepers deliberately moving hives to heather moors (Hooper, 1991). However, in May of the following year, the mean distance dropped to 1 km, very similar to the results of this study and that of Couvillon *et al.* (2014a). Although the summer foraging distance difference between Brighton and Sheffield may be because the urban area in Sheffield is poorer in forage than Brighton; this is unlikely as the areas where the hives were kept were very similar residential areas with many houses with gardens and parks. The more likely explanation is that the countryside to the west of Sheffield is exceptionally rich in forage due to the heather moors. In contrast, the countryside around Brighton not only lacks heather moors or similar large flower patches, but is also dominated by intensive agriculture typical for present-day Britain (Robinson & Sutherland, 2002).

To our knowledge, the only other dance-decoding study looking at honey bee foraging from hives in an urban location is that of Waddington *et al.* (1994). Their data were collected in suburban areas of Miami (FL) and Riverside (CA), USA, in spring. As these areas have considerably different environment and climate to the UK, a straightforward comparison is confounded. However, with this reservation, the short foraging distances reported (0.7–1.4 km) are in close agreement with the spring data in and around Brighton (in accordance with our results and those of Couvillon *et al.* 2014a) and Sheffield (Beekman & Ratnieks, 2000).

What does foraging by urban honey bees tell us about urban areas? The low foraging distances shown by our urban bees indicate that colonies were able to find high-quality forage nearby (Seeley, 1994; 1995), and for the most part did not need to visit the countryside, even though it was within foraging range. They also indicate that urban bees may not make a significant contribution to agricultural pollination, especially in spring

when two of the most important UK crops benefitting from bee pollination, oilseed rape and apples, are in bloom (Mwebaze *et al.*, 2010). However, our study was conducted in only one urban location and so should be replicated in other locations before generalizations are made.

Urban areas in the UK contain many green spaces, including domestic gardens (Loram *et al.*, 2007), which, collectively, are a large and important resource for wildlife (Davies *et al.*, 2009; Goddard *et al.*, 2010; Cameron *et al.*, 2012). Indeed, many gardeners practice wildlife-friendly gardening, which, among other things, includes cultivating garden plants attractive to flower-visiting insects (Table A1.57 in Mew *et al.* 2003). The urban area surrounding our study location was largely residential, but even residential areas in the UK are substantially green, as most homes (87 %, Davies *et al.* 2009) have a garden. The surrounding area also included several public parks, sports grounds including a golf course, and allotments, where honey bees could contribute to crop pollination. In addition to garden plants, many urban trees, such as limes (*Tilia* spp.), willows (*Salix* spp.,) and maples (*Acer* spp.), can also serve as important nectar and pollen sources (Batra, 1985; Pawlikowski, 2010; Çelemli, 2012). In autumn (September – October), the most important source of nectar and pollen is flowering ivy (*Hedera helix* and *H. hibernica*), which is widespread in Britain and abundant in the study area (Metcalfe, 2005; Chapter 8: Garbuzov & Ratnieks, 2014b).

Are urban areas better than rural areas? Honey bees are very sensitive to foraging economics (Seeley, 1995; Seeley *et al.*, 2000; 2012). As a result, flower patches in the closer urban area would be selected over equal forage-quality patches in more distant rural areas. Therefore, our data showing that most foraging is in the urban area does not mean that this area is better overall, but it does show that it is relatively better after distance is taken into account, as distance is one of the most significant costs associated with a honey bee decision-making in foraging.

Chapter 11

Honey bee colonies show limited foraging on oilseed rape, a potential source of neonicotinoid contamination

Mihail Garbuzov, Margaret J. Couvillon, Roger Schürch, Francis L. W. Ratnieks

Abstract

Neonicotinoid insecticides used to treat the seeds of bee-attractive crops occur in trace amounts in nectar and pollen. This may harm social bees and other pollinators. Recent laboratory and semi-field studies on colony-level effects of neonicotinoids assumed exclusive or near-exclusive levels of colony foraging on a treated crop. But is this a realistic assumption? We monitored six honey bee colonies over two springs (April – May 2011/12) in two neighbouring locations (urban and rural) to quantify foraging on oilseed rape, the most widespread bee-attractive crop in the UK, by decoding waggle dances and trapping pollen. The study area was representative of the UK agricultural landscape in that the percentage area cover of the blooming oilseed rape fields around the rural location was similar to the national average (3.3-3.9% vs 3.1%). The amount of foraging on oilseed rape fields, as indicated by dance decoding, was variable, but low, 0-0.02% for the urban and 2-26% rural location. Almost all foraging, 91-99%, was within 2 km, even though honey bees can forage at distances of over 10 km. Pollen trapping in 2012 supported the dance decoding results, with oilseed rape pollen comprising 14% of pollen pellets collected by foragers from rural and 4% from urban hives. Possible harm to bees has resulted in the European Commission imposing a two-year moratorium on the use of neonicotinoids on bee-attractive crops from 2013. Our results have implications for policy as they cast doubt on the generality of some previous studies on colony-level effects

of social bees conducted in laboratory and semi-field settings. Future attempts to estimate these effects should take into account the possibility of lower levels of foraging on treated mass-flowering crops, such as oilseed rape.

Introduction

Oilseed rape (*Brassica napus*) is a major crop, with 35 million ha grown worldwide in 2012/13, yielding 61 million tonnes of oil (USDA, 2013). In the UK, oilseed rape acreage has trebled in the past 30 years to 756,000 ha in 2012 (3.1% of land area) and is now the third most important arable crop after wheat and barley (DEFRA, 2012). Oilseed rape is cultivated in dense monocultures, which at flowering become an important potential resource to honey bees, bumble bees and other flower-visiting insects that feed on nectar and pollen (Fussell & Corbet, 1991; Howlett *et al.*, 2009; Rollin *et al.*, 2013). For example, flowering oilseed rape improves bumble bee early colony growth (Westphal *et al.*, 2009) and increases worker density at a landscape scale (Westphal *et al.*, 2003). Diekötter *et al.* (2014) have shown that oilseed rape is associated with greater species richness of solitary cavity-nesting bees and wasps. In this respect, it may be advantageous as an additional source of forage. However, to combat herbivorous insects, almost all oilseed rape (e.g. 98% in the UK, Garthwaite *et al.*, 2012) is treated with systemic neonicotinoid insecticides applied as a seed dressing, with residues at potentially harmful concentrations present in nectar and pollen (Table 6 in EFSA, 2012). Oilseed rape is a prime route by which bees may ingest these chemicals in the UK, where it is the most widespread bee-attractive crop, and is also important in other countries, given that the UK acreage is only 2% of the world total.

There is currently much debate over the effects that neonicotinoid residues in nectar and pollen have on bees (Blacquière *et al.*, 2012; Goulson, 2013; van der Sluijs *et al.*, 2013). Although the effects on individual bees resulting from a single feeding event at an environmentally-realistic dose are not lethal (Suchail *et al.*, 2000), there is a concern that chemical concentrations may bio-accumulate (Rortais *et al.*, 2005; Byrne *et al.*, 2014)

and/or cause sub-lethal effects, such as impaired learning or foraging ability (Mommaerts *et al.*, 2010; Cresswell, 2011; Schneider *et al.*, 2012), which may, in principle, translate into adverse colony-level and, ultimately, population-level effects.

In May 2013 the European Commission imposed a precautionary 2-year moratorium on the use of three neonicotinoids (imidacloprid, thiamethoxam, and clothianidin) on bee-attractive crops in the European Union (European Commission, 2013). This is intended to allow time for further research developments before the next review of scientific evidence in 2015. However, there remain important gaps in our knowledge (Cresswell *et al.*, 2012). Most recent key studies investigating colony-level effects in social bees were done under laboratory or semi-field conditions. One challenge in these studies is to choose doses that are relevant to field exposure, including the concentration, duration of exposure, and choice. For example, Henry *et al.* (2012) administered 1.34 ng of thiamethoxam in a single feeding to individual honey bees - an amount that a bee would consume during a whole day of foraging. Other studies, this time on bumble bees, assumed great or even exclusive foraging on a treated crop either by providing no alternative choice during the treatment phase (Whitehorn *et al.*, 2012), or by using amounts of treated sucrose solution equivalent to about half of the daily colony intake (Gill *et al.*, 2012). However, under field conditions, the bees often have a large choice of nectar and pollen sources. Indeed, there is the possibility that treated crops may repel bees (Eiri & Nieh, 2012; Easton & Goulson, 2013). In a statement evaluating the recent evidence for the impact of neonicotinoids on bees, the European Food Safety Authority concluded that it remains uncertain to what extent such exposure regimes are representative of field conditions (EFSA, 2012).

In this study we quantify honey bee foraging on spring-blooming oilseed rape by decoding waggle dances and pollen trapping from hives in neighbouring urban and rural locations in a landscape with many oilseed rape fields within foraging range. Dance decoding showed variable, but relatively low foraging in oilseed rape fields, ranging from 0-0.02% (urban) to 2-26% (rural). Pollen analysis was in broad agreement with these results at 4% (urban) and 14% (rural). Foraging on oilseed rape fields declined rapidly

with distance from the hives and approached zero at >2 km. These results should help future studies of insecticide effects on social bees to include field-relevant levels of colony exposure.

Methods

Study honey bee colonies and landscape

We used three honey bee colonies in a rural location (Laboratory of Apiculture & Social Insects, University of Sussex, lat.: 50.863889, long.: -0.083830386) and three in an urban location (Dorothy Stringer School, Brighton, lat.: 50.849370, long.: -0.14167996) 4.5 km to the south-west. The colonies were housed in indoor glass-walled observation hives containing three medium and one deep Langstroth frames, an egg-laying queen, brood of all ages, and c. 2000-5000 workers.

Most oilseed rape (98% in 2012) in the UK is 'winter rape' being sown in late summer or autumn and flowering the following spring (DEFRA, 2012). The rest, 'spring rape' (2% in 2012), is sown in spring to flower in summer. In 2011 and 2012, we rented a light aircraft to conduct aerial surveys of the study area twice each spring to locate and photograph all oilseed rape fields within 6 km of the two study apiaries. These fields stand out due to the bright yellow flowers and are visible at long distances, several kilometres, when flying at c. 2000-2500 ft altitude. The fields were then located on the Sussex Habitat Framework map, a georeferenced land type database provided by the Sussex Biodiversity Records Centre, to determine their exact positions, areas, and distances to the apiaries using Geographic Information System software (ArcGIS Desktop 10, Esri, USA). Oilseed rape was 3.33% and 3.89% of the area within 6 km of the rural apiary in 2011 and 2012, respectively, and 1.19% and 2.34% for the urban apiary, making the amount of oilseed rape in the rural area close to the national average (3.1%) (DEFRA, 2012). In addition, a cluster of adjoining fields of flowering linseed (*Linum usitatissimum*) fields (47 ha) was

spotted in 2011 and mapped, as it is also a bee-attractive crop (Abrol & Kotwal, 1996). No other bee-attractive crops were seen during the study period in the study farmland area, which was otherwise dominated by wheat, barley and grazing land.

Waggle dance analysis

Concurrent to mapping the oilseed rape fields, we monitored honey bee foraging in each hive using video cameras. Using the videos we decoded in total 1646 waggle dances from the six observation hives during the main period of oilseed rape flowering (April & May) in both 2011 and 2012. Methods followed Couvillon *et al.* (2012), where four waggle runs per dance were decoded to obtain each dance's mean duration, which encodes distance, and angle, which encodes direction. Distance was estimated using a Bayesian linear calibration model built for our honey bee population and landscape (Schürch *et al.*, 2013), which takes into account the imprecision inherent in the honey bee dance. Probability distributions for distance estimates can then be combined with probability distributions representing the variability in the second vector component, the direction (Schürch *et al.*, 2013). In this way we were able to map the foraging locations shown by the dances in a manner that includes the uncertainty in the dance vector (Schürch *et al.*, 2013). This methodology also allowed us to determine confidence intervals for our estimates of the proportion of dancing for oilseed rape fields.

Pollen collection and identification

Pollen samples were collected from returning foragers during April and May 2012 by placing pollen traps (5.0 mm plastic mesh; E.H. Thorne, UK) at the entrance of each hive for 1 h at approximately weekly intervals. The mesh knocks pollen pellets from the corbiculae of returning foragers as they pass through.

Pollen pellets were first categorized by colour. Up to five pollen pellets per colour per sample (from each hive on each data collection day) were mounted on slides and examined using a light microscope at 400× magnification (Zeiss Axiophot, Oberkechen, Germany). In a few cases when pellets of one colour in a sample were not monofloral, the number of pellets of each morphotype was estimated from its proportion among the five pellets examined. Oilseed rape pollen was identified by reference to samples collected locally from oilseed rape flowers. The remaining morphotypes were not identified, with the exception of dandelion (*Taraxacum officinale*), which was identified from a combination of morphology (Marciniuk & Rudzińska-Langwald, 2008) and pellet colour (Kirk, 2006).

Results

Amount of foraging on oilseed rape indicated by waggle dance analysis

Figure 11.1 maps the foraging locations as probability distributions based on dance decoding. There was effectively no overlap in the foraging between the two apiaries. In the urban apiary, most foraging (93%) was within 1 km, and almost all (99%) within 2 km. In the rural apiary, on average 60% of foraging was within 1 km, with more foraging occurring at 1-2 km and concentrated around oilseed rape fields. The distortions of the dance density distribution by the oilseed rape fields (Fig. 11.1) show that this crop is more attractive, on average, than the surrounding landscape. However, the total proportion of foraging on oilseed rape fields was limited. In the urban location, the mean proportions were 0% for April in both years, and 0% and 0.02% for May in 2011 and 2012, respectively. In the rural location, the mean proportions during the two years were 2.2% (2011) and 21.8% (2012) for April and 8.0% (2011) and 26.1% (2012) for May (full data including confidence intervals are given in Table 11.1).

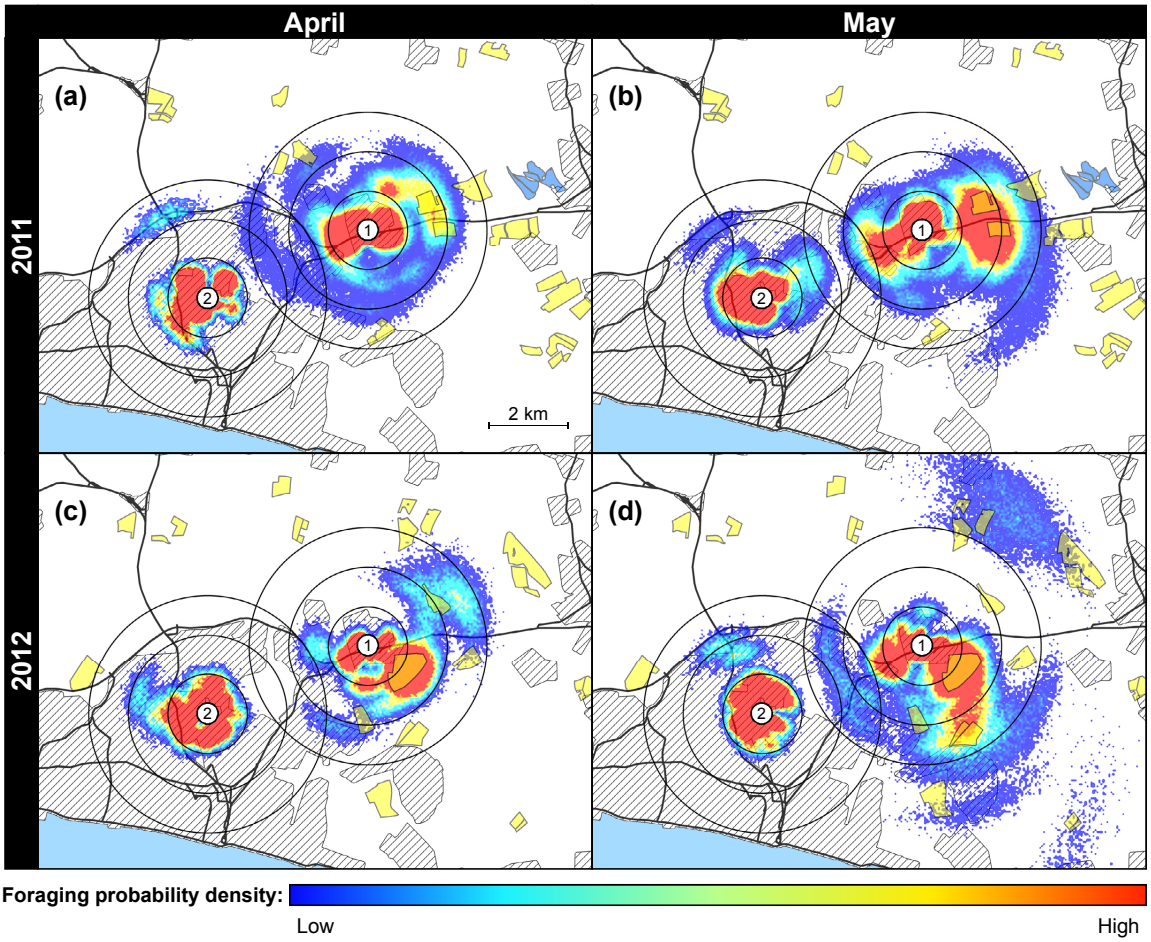


Figure 11.1. Probability density distributions of honey bee foraging from (1) the rural apiary at Laboratory of Apiculture & Social Insects and (2) the urban apiary at Dorothy Stringer School in relation to oilseed rape (yellow) and linseed (darker blue, 2011 only) fields in April & May 2011 (a,b) and 2012 (c,d). Landscape comprised a mixture of rural (white) and urban (hatched) areas bordered by the English Channel to the south (lighter blue). Circles around apiary locations are 1, 2 and 3 km buffers. Colour spectra show the range of foraging probabilities, as determined by simulated waggle dance locations, binned into 25 × 25 m quadrats, from blue (1) to red (620-6985, depending on dataset).

Table 11.1. Estimated % of foraging on oilseed rape by rural (LASI) and urban (DS) hives

	% [a] of foraging on oilseed rape	95% CI [b] lower limit	95% CI [b] upper limit	Number of dances
Laboratory of Apiculture & Social Insects (LASI)				
2011 April	2.23%	1.17%	4.08%	460
May	7.97%	5.57%	11.26%	362
2012 April	21.84%	15.94%	29.15%	150
May	26.14%	20.63%	32.50%	209
Dorothy Stringer School (DS)				
2011 April	0.00%	-	-	61
May	0.00%	-	-	234
2012 April	0.00%	-	-	94
May	0.02%	0.00%	5.79%	76

[a]Percentage among simulated locations

[b]Agresti-Coull (Brown *et al*., 2001) 95% confidence intervals for binomial proportion, where *p* (number of simulated locations within fields) and *n* (total number of simulated locations) are scaled back to the number of dances

As part of crop rotation and pest management, farmers generally do not plant oilseed rape in the same field in consecutive years. This can be seen in the field locations in Figures 11.1 and 11.2, which all change from 2011 to 2012. Honey bees are known to make economic foraging decisions, with greater foraging distance increasing costs and having an effect on decisions to forage and recruit nestmates to foraging locations via the waggle dance (Seeley, 1994; Cresswell *et al.*, 2000; Seeley *et al.*, 2000). Thus, the locations advertised by waggle dances do not represent all foraging locations currently being used by a colony, but only the most profitable locations to which the recruits are being directed (reviewed in Dyer, 2002). The greater amount of foraging on oilseed rape in 2012 from the rural apiary seems to be a consequence of crop rotation, which resulted in a large field of oilseed rape (61 ha) only 0.7 km from the rural hives at its closest point. This one field accounted for almost a quarter (22.7%) of all spring foraging and almost all (93%) spring foraging on oilseed rape. In 2011 the two closest fields were adjacent at distances of 1.3 and 1.7 km, and had a combined area of 46 ha. They received only 4.7% of all spring foraging, but 98% of total spring foraging on oilseed rape. Figure 11.2c shows that the amount of foraging per unit area of oilseed rape declines greatly with distance. There was almost zero foraging at distances over 2 km, which demonstrates that oilseed rape cannot be profitably exploited at greater distances at this time of year in relation to other available forage. Similarly, the fields of linseed at 4.1 km from the rural apiary did not receive any visits.

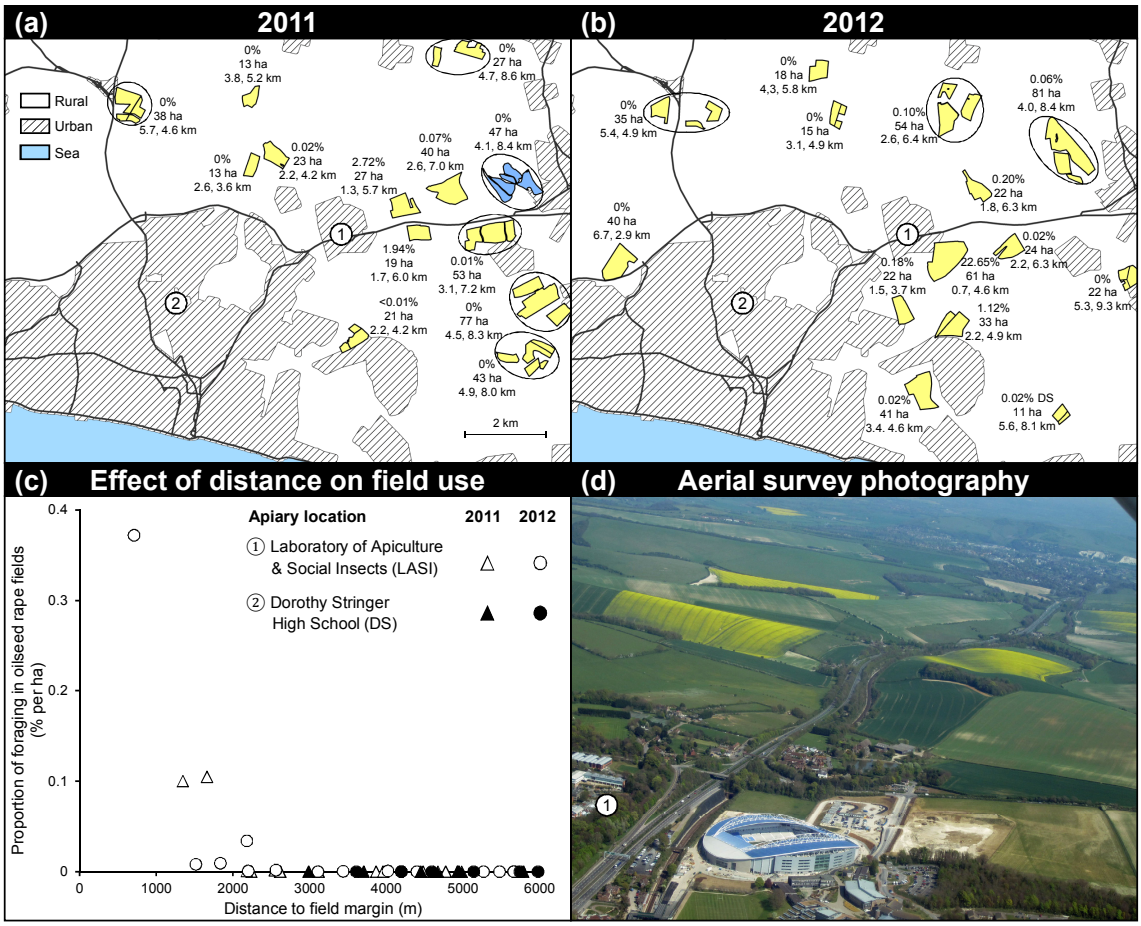


Figure 11.2. Percentage of total spring (April & May) foraging on particular oilseed rape (yellow) and linseed (darker blue, 2011 only) fields, in addition to field area and distances from the Laboratory of Apiculture & Social Insects (LASI) and Dorothy Stringer High School (DS) apiaries, respectively, in 2011 (a) and 2012 (b). Circled groups of neighbouring fields are treated as one unit. All foraging was from colonies at the LASI apiary, with the exception of one field in 2012 (marked DS) in which the 0.02% foraging level was from the DS apiary. (c) Proportion of total foraging per hectare of field or field group as a function of apiary distance to the closest field margin. (d) Aerial photo taken on 19/04/2011 showing four fields of oilseed rape on both sides of the A27 highway east of the rural apiary location (marked 1 on photo).

Amount of foraging on oilseed rape indicated by pollen analysis

The proportion of oilseed rape pollen pellets was 13.8% (total n = 3436) and 3.8% (total n = 1344) from the rural and urban hives, respectively. Hives in each location were similar in the proportions of oilseed rape pollen collected, being 13.4%, 13.3% and 16.8% among the three rural hives and 2.2%, 5.1% and 6.1% among the three urban hives. Similarly, Odoux *et al.* (2012) found that the oilseed rape pollen comprised no more than 29% of the total pollen collected by honey bees in an agricultural landscape where oilseed rape covered 5% of the land within 2.5 km of the apiary. However, both our data and those of

Odoux *et al.* (2012) are likely to be overestimates due to possible false positives, as pollen of other Brassicaceae species can be difficult or impossible to distinguish from oilseed rape (Odoux *et al.*, 2012). This may also explain why we detected oilseed rape pollen in the urban samples even though foraging in oilseed rape fields was not indicated by dance decoding.

Overall the pollen data support the waggle dance data and strengthen the conclusion that oilseed rape did not dominate foraging. The remaining pollen was categorized into 31 morphotypes, 20 from the rural samples and 22 from the urban. The leading four morphotypes accounted for 89.1% and 72.1% of all pollen in the rural and urban locations, respectively (Fig. 11.3). A common wildflower, the dandelion (*Taraxacum* sp.), was the second most important pollen type in the rural location (26.5%) and fifth (6.6%) in the urban location. Oilseed rape was the third most important in the rural and tenth in the urban location. The remaining types were not identified, but appeared to be mainly Rosaceae. This matches casual observations that in spring there are many hawthorn (*Crataegus monogyna*) and blackthorn (*Prunus spinosa*) bushes in bloom, as well as wild and cultivated fruits, such as cherries and plums (*Prunus* spp. and their cultivars), all in this family.

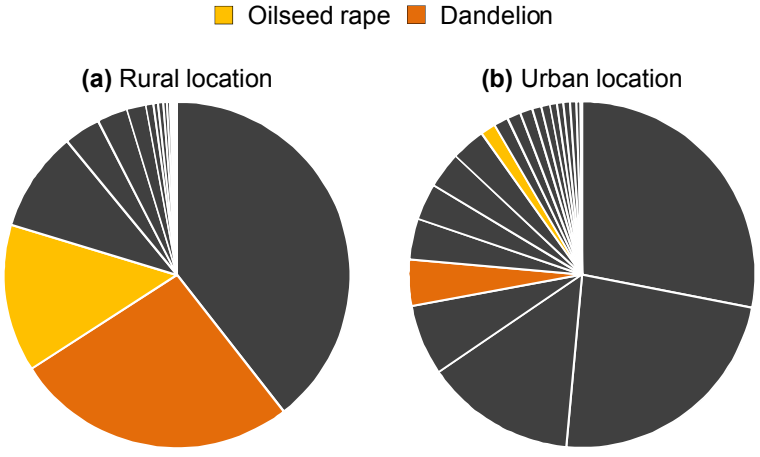


Figure 11.3. Diversity of pollen morphotypes based on pollen pellets collected by bees from three hives each at the rural (a) and urban (b) apiaries. Only pollen of oilseed rape (*Brassica napus*) and dandelion (*Taraxacum* sp.) was identified. The remaining pollen morphotypes are shown in grey and were not identified.

Discussion

Overall, our data show that spring-flowering oilseed rape is a variable forage resource for honey bees, and was a relatively small fraction of both the pollen samples and the foraging

locations shown by dance decoding. Honey bees are capable of foraging at distances of over 10 km (Beekman & Ratnieks, 2000; Ratnieks, 2007). As a result, the colonies at both the rural and urban apiaries had many oilseed rape fields within range. In our study, however, most foraging was within 2 km of the hives, whether to fields of oilseed rape or not.

What do our results add to the debate about the use of neonicotinoids to treat the seeds of oilseed rape and other flowering crops? One of the key requirements in the design of experiments investigating colony-level effects of insecticides on social bees is the use of environmentally-realistic doses (Cresswell *et al.*, 2012). However, our data indicate that the levels of colony exposure may have been overestimated. For example, Bryden *et al.* (2013) fed bumble bee colonies with neonicotinoid-treated sucrose solution under laboratory conditions with no access to the outside world, thus assuming the colonies forage exclusively on a treated crop. Whitehorn *et al.* (2012) used a similar feeding regime, with the exception that colonies were moved to the field after the treatment phase. Gill *et al.* (2012) allowed the bees to forage outside, but provided a treated solution to the colonies with "a similar amount of active ingredient as if they had been foraging exclusively on a crop with 5 ppb imidacloprid in the nectar". Henry *et al.* (2012) constructed models predicting honey bee colony failure based on individual-level harm on homing ability and the proportion of foragers in a colony exposed to a treated crop, which was assumed to be 50-90%.

In reality, the levels of colony exposure to a treated crop are variable, but may often be lower than assumed above, even in landscapes where that crop is abundant, as there are often many alternative flowers available. Using pollen analysis, Pettis *et al.* (2013) showed that honey bee foraging on flowering agricultural crops, where the hives are placed into or beside the crop for pollination, ranges from nearly 100% (almond) to nearly 0% (e.g. watermelon, pumpkin). With regard to oilseed rape, most of the UK crop is planted in late summer or autumn to bloom next spring, when honey bee foraging distances are at their seasonal minimum, indicating high floral abundance in the environment (Beekman & Ratnieks, 2000; Couvillon *et al.*, 2014a). Indeed, in our study a

common wildflower, the dandelion, was approximately twice as important a pollen source than oilseed rape in the rural location (26.5% vs 13.8%), where most of the foraging on oilseed rape occurred. Although wildflowers, such as the dandelion, may also become contaminated with, and thus serve as sources of neonicotinoids to bees, this has only been detected in plants growing nearby agricultural fields in the USA (Krupke *et al.*, 2012). Thus, foraging on wildflowers is likely not to be a major route of exposure.

Summer-flowering oilseed rape may present a different picture. Summer is a more challenging foraging season than spring for honey bees in the study area, with mean foraging distances several times greater (Couvillon *et al.*, 2014a). If the same fields of oilseed rape had been in bloom in July, they would almost certainly have received more foragers from the study hives. Hayter and Cresswell (2006) showed that summer-flowering oilseed rape can have c. 300× greater bee density than spring-flowering. This would have increased its potential benefit as a food source, but also increased the level of exposure to insecticides.

Under field conditions, it is also possible that pesticide residues in nectar and pollen may themselves help to reduce foraging on treated crops by acting as repellents. Some insecticides are long known for their repellent effects on pollinators [e.g. pyrethroids (Thompson, 2001 and references therein)]. But in the case of neonicotinoids the situation is less clear. An early study found that honey bees take longer to return to a syrup feeder treated with the neonicotinoid imidacloprid (Bortolotti *et al.*, 2003). However, the concentrations used were 100 ppb or more, which are ten or more times greater than the maximum detected in nectar (Table 6 in EFSA, 2012). More recently, Eiri and Nieh (2012) showed that imidacloprid at more realistic doses, as low as 0.21 ng per honey bee, raises the response threshold to sucrose via the proboscis extension reflex, and lowers the tendency to make waggle dances. If bees foraging on a treated crop made fewer or shorter dances, this could reduce the recruitment of nestmates to a treated area. Similarly, Easton and Goulson (2013) found that pan traps containing imidacloprid at a concentration of 1 ppb had a repellent effect on both flying beetles and flies and a concentration as low as 0.01 ppb still repelled flies. It is possible that the repellent effects

of neonicotinoids could play a role under field conditions, although further research is needed to determine whether this is the case or not.

How can our results inform future studies and policy? The decision on whether to permit the use of neonicotinoid seed treatments on bee attractive crops should be based on a careful weighing of their benefits in reducing insect damage and all possible negative effects to bees and the wider environment (Goulson, 2013). However, relatively little is known about their effects in the environment and on species other than the honey bee, *Apis mellifera*, and one bumble bee, *Bombus terrestris* (Goulson, 2013). Indeed, the current EU moratorium restricts neonicotinoid use only on bee-attractive crops (European Commission, 2013), highlighting that possible effects on bees are at the forefront of the issue. The effects on social bee colonies can most reliably be determined in field experiments such as that performed by (Pilling *et al.*, 2013), showing only a low risk to honey bee colonies exposed to treated oilseed rape and maize in France. In contrast, the relevance of laboratory or semi-field studies to field conditions should be interpreted with caution, especially where a single dose has been used, given that several factors affect field exposure and that there is variability and uncertainty in these factors. Our findings should help base future studies on more realistic levels of one of these factors, colony exposure, and highlight the fact that under field conditions bees will normally have a choice of forage sources.

Research Chapters

Part 5: Good Practice in Urban Beekeeping

Chapter 12

Lattice fence and hedge barriers around an apiary increase honey bee flight height and decrease stings to people nearby

Mihail Garbuzov, Francis L. W. Ratnieks

Abstract

Urban beekeeping is becoming more popular in the UK. One of the challenges faced by urban beekeepers is finding a suitable apiary location. Honey bees are often perceived as a nuisance, mainly due to their stinging behaviour. Here, we experimentally test the assumption that barriers around an apiary such as walls or fences, force the bees to fly above human height, thereby reducing collisions with people and, consequently, stinging. The experiment was conducted in two apiaries using two common types of barrier: a lattice fence (trellis) and hedge. Barriers were 2 m high, which is taller than >99% of humans and is also the maximum height allowed by UK planning regulations for garden fences or walls. We found that barriers were effective at both raising the mean honey bee flight height and reducing stinging. However, the effects were only seen when the barrier had been in place for a few days, not immediately after the barrier was put in place. Although this raises interesting questions regarding honey bee navigation and memory, it is not a problem for beekeepers, as any barrier placed around an apiary will be permanent. The effect of the barriers on raising bee flight height to a mean of c. 2.2-2.5 m was somewhat weak and inconsistent, probably because the bees flew high, mean of c. 1.6-2.0 m, even in the absence of a barrier. As barriers can also reduce wind exposure, improve security and are inexpensive, we recommend their use around urban apiaries in places such as private gardens or allotments, where nuisance to humans is likely to be a problem.

Introduction

Although honey bee (*Apis mellifera*) hives are often kept in the countryside away from people and housing, many are also kept in urban and suburban areas. Indeed, urban beekeeping is becoming more popular (Benjamin & McCallum, 2011). For example, in London UK, the number of registered colonies doubled to more than 3,500 over the last 5 years (2008-13) and the number of beekeepers tripled (Alton & Ratnieks, 2013). This is an underestimate, since the registration is non-mandatory. One challenge to urban beekeeping is finding suitable apiary locations. Numerous general criteria exist for choosing a good apiary location, including proximity to rich nectar sources, vehicle access, shelter from strong wind, sunlight, good air circulation to avoid frost pockets, and water drainage (Morse, 1972; Cramp, 2008). However, for an urban beekeeper, perhaps the most important is seclusion from fellow humans (Burgett *et al.*, 1978).

Honey bees are often perceived as dangerous due to their stinging behaviour. Being stung by a honey bee worker is painful (Schmidt, 1990), but the main danger is to the small proportion of people (0.15 to 5.0%) who are allergic to hymenopteran venom, which can lead to anaphylaxis and in rare instances death (Schmidt, 1986; Neugut *et al.*, 2001). However, the risk is exceedingly small, as one is twice more likely to die from a lightning strike than from a bee sting (Schmidt, 1986). In the UK (England & Wales) in 2011, only two deaths were caused by "contact with hornets, wasps or bees", three times fewer than were caused by a "bite or strike by dog" (Office for National Statistics, 2012). Many people believe they are allergic to honey bee stings, when in fact they are not (Charpin *et al.*, 1992), probably because the normal reaction of a non-allergic person is often considerable, involving immediate pain, followed by local swelling and itching lasting a day or more (Vetter *et al.*, 1998). In any event, a sting from a worker honey bee is an unpleasant experience and one to be avoided.

Barriers, such as fences, hedges or buildings, surrounding an apiary are often recommended in order to force the bees to fly above human height (Caron, 1976a in Burgett *et al.*, 1978; Cramp, 2008), thereby lessening the chance that foraging bees leaving

or returning to their hives will bump into humans. As colliding bees may become entangled in hair or clothing, and often result in ineffective attempts to brush then off, this can easily lead to stinging. Here, we perform the first experimental test of this recommendation, using two types of barrier: a wooden lattice fence (trellis) and a hedge.

Methods

Experimental setup and procedure

The study was conducted using experimental apiaries set up at two locations: Wakehurst Place, West Sussex, UK (lat: 51.067163, long: -0.090604484) and Plumpton College, East Sussex, UK (lat: 50.911375, long: -0.081055820). Four strong honey bee colonies were used in each apiary.

The apiaries were located with a wooden shed and a brick wall on two sides (Wakehurst) or a large metal barn on one side (Plumpton), with the hives 50 cm from the building and facing away (Figs. 12.1 ,12.2). On other sides temporary barriers of either lattice fence or hedge were positioned 1 m from the hives, and could be swapped or removed within a few minutes as needed during the experiment. This was referred to as the "current" treatment in the analyses. Honey bee flight heights were recorded at four distances on the far side of the barrier at 1, 3, 6 and 16 m at Wakehurst. At Plumpton 8 m was used instead of 6 m due to the land layout, as there was a ditch at 6 m (Fig. 12.1b). Flight heights were recorded at each of 12 barrier × distance combinations on each day, and repeated on six non-consecutive days in the periods August to October, 2011 (Wakehurst) and July to September, 2012 (Plumpton). In addition, each of the three barrier treatments (lattice, hedge or no barrier) was left in place for multiple days (mean 9.1, range 2-23), before two of the six experiment days in each dataset; this was included as the "pre-treatment" in the analyses. At Wakehurst, due to the layout of the garden in which the apiary was located, only one direction could be investigated, but in the

Plumpton apiary, the same procedure was replicated in two directions at 90° to each other, but the hives were not rotated, such that their entrances were always facing direction 1 (Fig. 12.1b). Thus, in total, three comparable datasets were obtained from two apiaries.

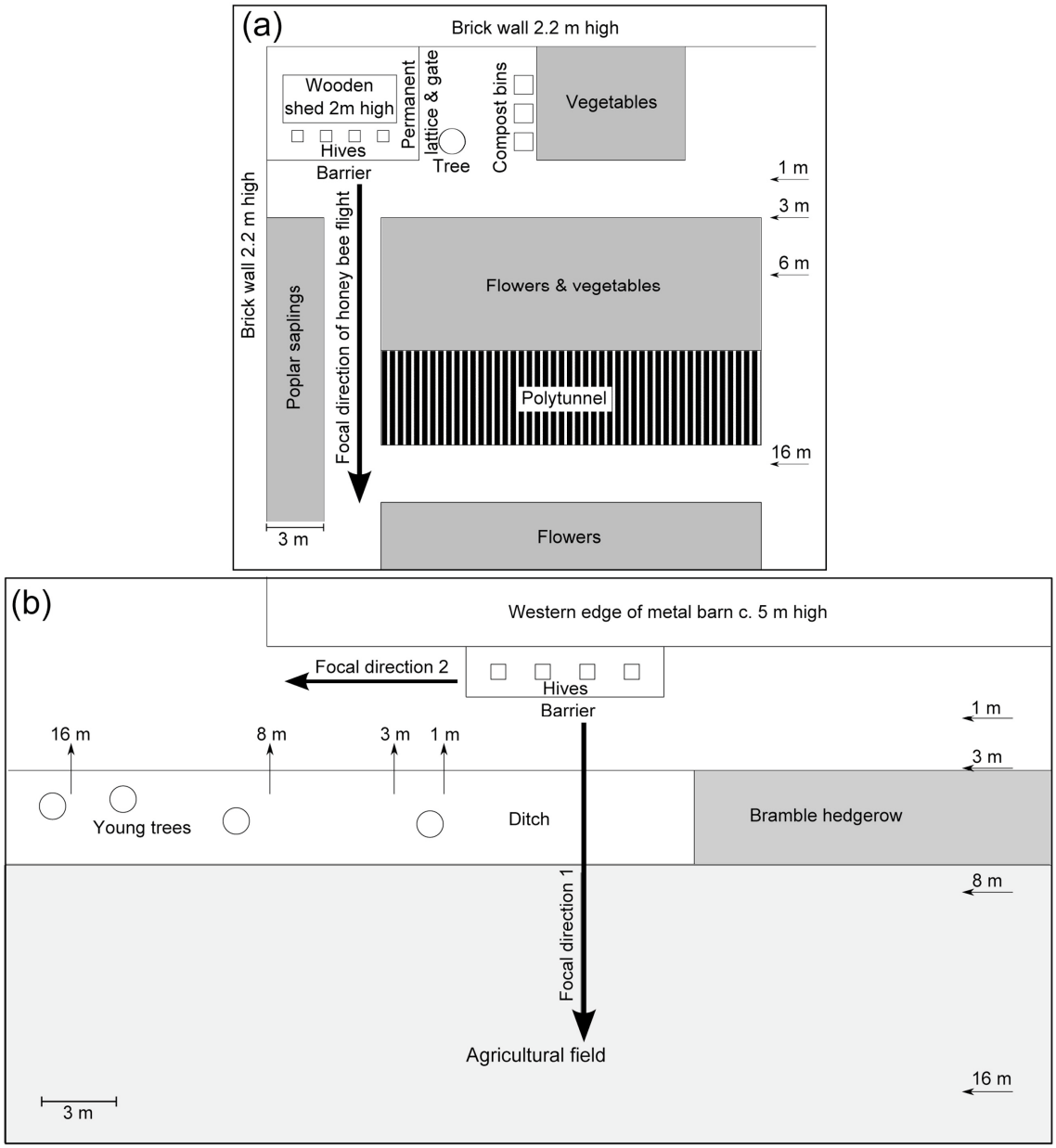


Figure 12.1. Layout of the apiary and surrounding land at: (a) Wakehurst Place and (b) Plumpton College. Small arrows mark the positions of the video camera at four distances perpendicular to the focal directions of honey bee flight.

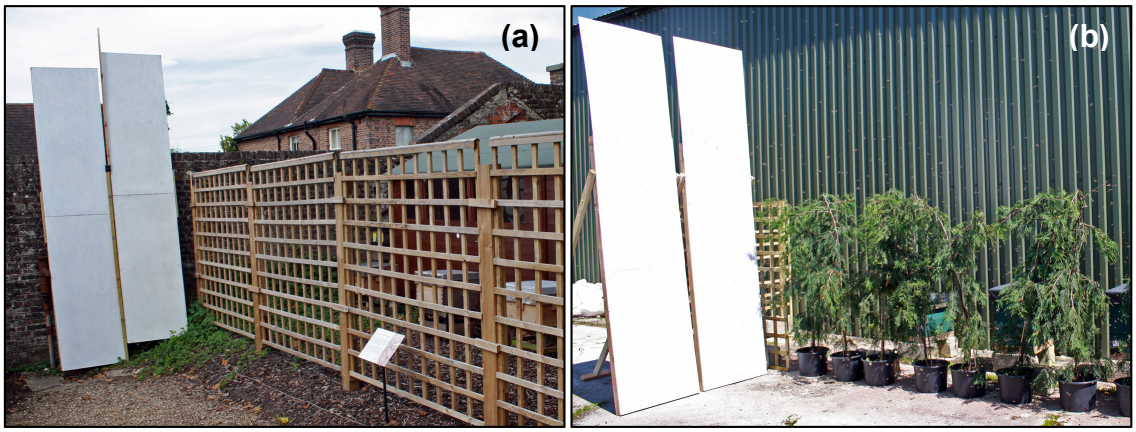


Figure 12.2. Experimental apiary setup showing white-painted plywood screens next to the lattice fence barrier (a, Wakehurst) and the hedge (b, Plumpton).

Barrier design

The lattice fence barrier (AVS Fencing Supplies Ltd; UK) was made of 1.83 × 1.83 m panels consisting of 11 horizontal and 11 vertical wooden planks 3.6 cm wide spaced at equal intervals and resulting in 100 14.3 × 14.3 cm empty gaps per panel, or 61.4% gap space.

The hedge barrier was made of large freshly-cut birch (*Betula* sp.) branches with leaves at the Wakehurst apiary and young potted Leyland cypress trees (*Cupressus* × *leylandii*) at the Plumpton apiary. The amount of empty space was comparable between the two types of hedge and to that in the lattice fence.

All barriers were positioned 1 m in front of and perpendicular to the hive entrances (Figs. 12.1, 12.2) and were 2 m high. To achieve this height the lattice panels were raised by 17 cm from the ground and hedge plants and branches were trimmed. In the Wakehurst apiary and in direction 1 in the Plumpton apiary, the length of the barrier was 8 m, while in direction 2 at Plumpton the length was 2 m (Fig. 12.1).

Measuring flight heights

The flight paths of honey bees were recorded at each distance using a Sony HDR-CX130E video camera. Recordings were made sequentially at each distance and barrier treatment against a white-painted plywood screen (1.6 m wide × 3.5 m high), positioned perpendicular at the far end of the barrier and parallel to the focal direction of honey bee flight (Figs. 12.1, 12.2). The video camera was on a tripod at a height of 1.7 m and 20 m from the white background to reduce parallax error. The video was played back frame by frame on using QuickTime v. 7.7.3 on an Apple iMac computer with 19″ (16:9) screen. Flying bees could be seen clearly as black dots. The flight heights of 10 consecutive individual honey bees (both incoming and outgoing) at each of the 12 barrier × distance combinations on each experimental day were determined against a series of height markers on the white screen.

Measuring sting rate

Sting rate was measured by recording the number of stings to the experimenter (MG) during standardized trials, which involved simulating physical work by hitting a wooden post with a hammer for 2 min at 1 m from the barrier position. One trial was made at each of the 3 barrier treatments on each experimental day at each apiary.

Statistical analyses

Data were analysed using R v. 2.15.2 (R Development Core Team, 2012). The effects of current barrier, pre-treatment barrier, and distance from the barrier on honey bee flight height in each of the three full datasets (1 from the Wakehurst apiary, 2 from the Plumpton apiary) were analysed using generalized linear mixed-effect models (GLMM) with function *lme* (package *nlme*, Pinheiro *et al*., 2012), using the maximum-likelihood

estimation method. To account for putative non-independence of data within the same experimental day and to assess the need for a mixed effects model, date was included as a random effect in the model before testing the fixed effects. We first compared the generalized least squares model (without the random effect) with the random intercept model and with the random intercept and slope model. In each dataset addition of the random intercept to the model significantly improved the fit to the data ($P < 0.05$). However, further addition of the random slope did not improve the fit significantly (see below in Results). The significance of the main effects (distance, current barrier and pre-treatment barrier) and their interactions were tested using the top-down model selection protocol and the likelihood-ratio test, where the optimal model is arrived at by removing non-significant terms from the beyond optimal model (Zuur *et al.*, 2009).

The effects of current and pre-treatment barrier on the number of stings per trial were analysed using 2-way ANOVA, since the inclusion of date as random effect did not significantly improve the fit of the model. *Post-hoc* pairwise comparisons of levels within significant factors and interactions were carried out using Tukey's test (function *glht*, package *multcomp*, Hothorn *et al.*, 2008). All values reported are means ± standard error, unless otherwise stated.

Results

Effects of current barrier, pre-treatment and distance on honey bee flight height

Wakehurst apiary

The addition of date as random intercept significantly improved the fit of model ($L = 6.653$, $df = 1$, $P = 0.001$). However, the addition of random slope did not ($L = 5.074$, $df = 5$, $P = 0.407$). Therefore, date was retained as random intercept in the model selection process.

The optimal model contained distance (L = 8.183, df = 1, P = 0.004) and pre-treatment barrier (L = 8.805, df = 2, P = 0.012) as significant main effect terms. Current barrier was not a significant factor (L = 3.632, df = 2, P = 0.163). Flight height was higher at 3 m from the barrier (2.32 ± 0.06 m) than at 6 m (2.05 ± 0.06 m; P = 0.005) or 16 m (2.02 ± 0.06 m; P = 0.002) (Fig. 12.3a). All other pairwise differences between distances were non-significant (P > 0.05). Flight heights were also higher on days when the bees were pre-treated with lattice fence (2.31 ± 0.05 m), compared to either hedge (2.03 ± 0.05 m; P < 0.001) or no barrier (2.09 ± 0.05 m; P = 0.009). Hedge and no barrier pre-treatments were not different from each other (P = 0.682) (Fig. 12.3d).

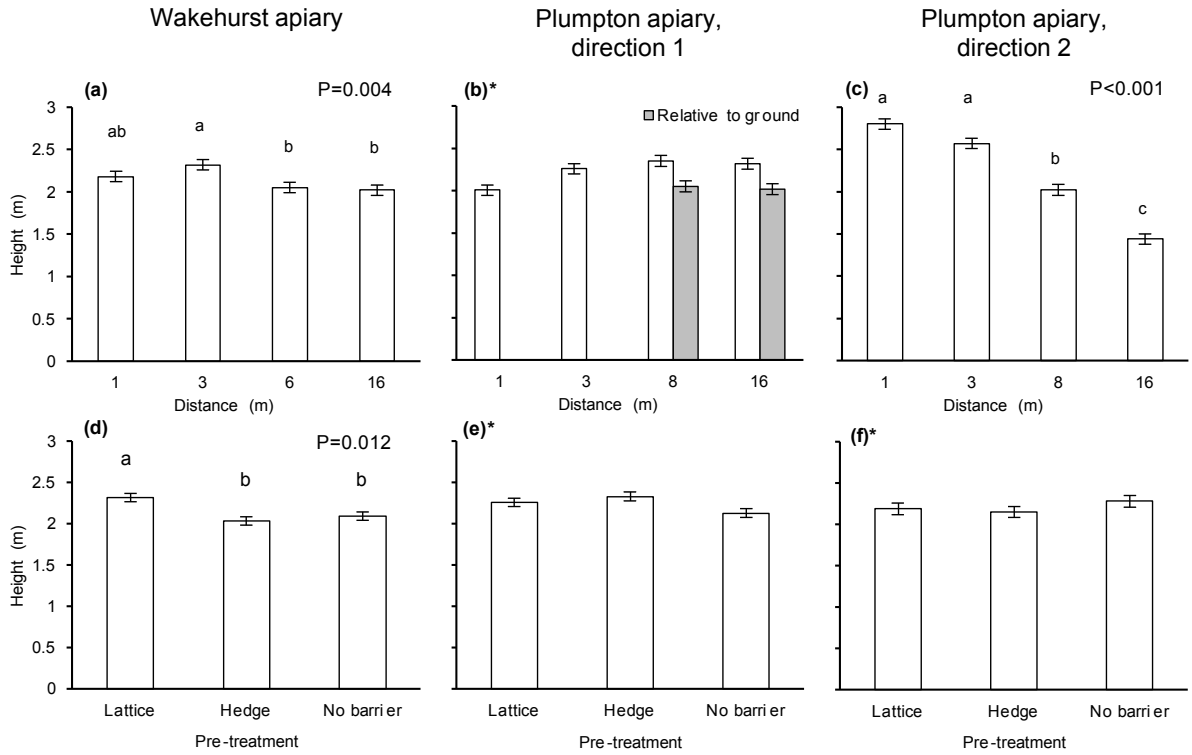


Figure 12.3. Effect of distance (a-c) and pre-treatment barrier (d-f) on mean honey bee flight height in the Wakehurst apiary (a,d) and the Plumpton apiary at directions 1 (b,e) and 2 (c,f). Letters above bars represent results of Tukey's *post-hoc* pairwise comparison test. * In (b), (d) & (f), significance of main effects was not tested due to their involvement in significant interactions (see Results, Fig 12.4). Height measurements are relative to the ground level under the apiary. In (b), the ground level at 8 m and 16 m was higher than at the apiary. Hence, the grey bars show bee fight height relative to the ground level at these distances. Bar heights are means ± standard error.

Plumpton apiary, direction 1

The addition of date as random intercept significantly improved the fit of the model (L = 7.002, df = 1, P = 0.008), however the addition of random slope did not (L = 6.674,

df = 5, P = 0.246). Therefore, date was retained as random intercept in subsequent model selection process.

The optimal model contained distance * pre-treatment (L = 27.534, df = 2, P < 0.001) and current barrier * pre-treatment (L = 16.027, df = 4, P = 0.003) as significant interaction terms. The significance of main effect terms was not tested further, as all of these were involved in at least one of the above significant interactions.

The results of selected pairwise comparisons (including all those with significant differences) within the distance * pre-treatment interaction are shown in (Table 12.1). In summary, there was evidence of higher flight heights at 1 m distance from the barrier when the bees were pre-treated with either lattice (2.17 ± 0.10 m; P = 0.056) or hedge (2.28 ± 0.10 m; P < 0.01), compared to no barrier (1.62 ± 0.10 m) (Fig. 12.4b). There was also some evidence of a similar, but weaker effect at 3 m distance (2.00 ± 0.11 m) from the barrier position (1 m *vs*. 3 m no barrier comparison, P = 0.302) (Fig. 12.4b).

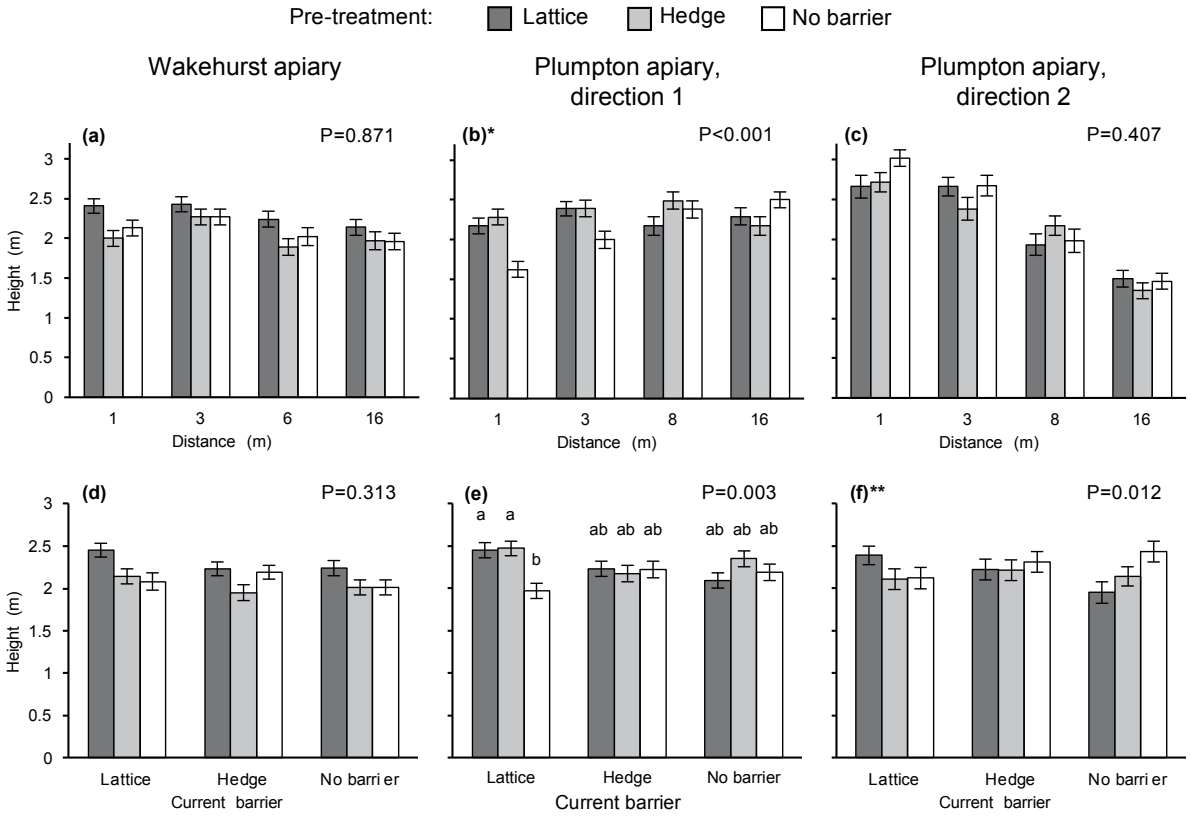


Figure 12.4. The effects of distance * pre-treatment (a-c) and current barrier * pre-treatment (d-f) interactions on honey bee flight height in the Wakehurst apiary (a,d) and the Plumpton apiary direction 1 (b,e) and 2 (c,f). Letters above bars represent results of Tukey's *post-hoc* pairwise comparison tests (* in (b), the results are found in Table 12.1; ** in (f), despite significant interaction, no pairwise comparisons between treatments were significant). Bar heights are means ± standard error.

Within the current barrier * pre-treatment interaction, flight height was greater after a quick change of barrier to lattice (current) and only when the bees were pre-treated to either lattice (2.45 ± 0.09 m; P = 0.049) or hedge (2.47 ± 0.09 m; P = 0.028), compared to the absence of a barrier (1.97 ± 0.09 m) (Fig. 12.4e). All other pairwise differences were non-significant (P > 0.05).

Table 12.1. Sub-set of the results of pairwise treatment comparisons, tested using Tukey's *post-hoc* tests, exploring the distance*pre-treatment interaction in the Plumpton apiary in direction 1. All significant (bold) and some non-significant pairs are shown; all pairs that are not shown are not significant at 5% confidence level.

Distance 1	Pretreatment barrier 1	*vs.*	Distance 2	Pretreatment barrier 2	P-value
1	Lattice	*vs.*	1	No barrier	0.056
1	Hedge	*vs.*	1	No barrier	**<0.01**
3	Lattice	*vs.*	1	No barrier	**<0.01**
3	Hedge	*vs.*	1	No barrier	**<0.01**
8	Lattice	*vs.*	1	No barrier	0.055
8	Hedge	*vs.*	1	No barrier	**<0.01**
16	Lattice	*vs.*	1	No barrier	**<0.01**
16	Hedge	*vs.*	1	No barrier	0.056
1	Lattice	*vs.*	3	No barrier	0.99
1	Hedge	*vs.*	3	No barrier	0.87
3	Lattice	*vs.*	3	No barrier	0.44
3	Hedge	*vs.*	3	No barrier	0.44
3	No barrier	*vs.*	1	No barrier	0.30
8	No barrier	*vs.*	1	No barrier	**<0.01**
16	No barrier	*vs.*	1	No barrier	**<0.01**
8	No barrier	*vs.*	3	No barrier	0.25
16	No barrier	*vs.*	3	No barrier	**0.03**

Plumpton apiary, direction 2

The addition of date as random intercept on the fit of model was marginally non-significant (L = 3.808, df = 1, P = 0.051). However the addition of random slope had clearly non-significant effect (L = 3.272, df = 5, P = 0.658). The decision was taken to retain date as random intercept in subsequent model selection process, because its non-significance was marginal and because it was also retained in the models analysing two other datasets.

The optimal model contained distance as main effect (L = 195.376, df = 1, P < 0.001) and current barrier * pre-treatment interaction (L = 12.844, df = 4, P = 0.012) as significant terms. The significance of the main effects of current barrier and pre-treatment barrier was not tested, as these were involved in the significant interaction.

Flight height tended to decrease with distance (Fig. 12.3c); although it was not significantly different between 1 m (2.80 ± 0.07 m) and 3 m (2.57 ± 0.08 m; P = 0.094), it was significantly different from both 8 m (2.08 ± 0.08 m) and 16 m (1.44 ± 0.06 m) (all P < 0.001).

Although the current barrier * pre-treatment interaction was significant in the final optimal model, no pairwise differences turned out significant (all P > 0.05). A qualitative look at the interaction (Fig. 12.4f) suggests that it is similar to the same interaction in direction 1 (which is significant in that dataset), as the flight height tended to be greater when the barrier was changed to lattice (2.39 ± 0.11 m) compared to no barrier (1.95 ± 0.13 m), but only when the bees were pre-treated to lattice (P = 0.188, lowest P-value of all pairwise comparisons).

Effects of current barrier and pre-treatment on the sting rate

In the Wakehurst apiary, 0 stings were recorded in a total of 18 2-minute trials. As a result, no further analyses were performed. In the Plumpton apiary, 10 stings in total were recorded using the same procedure. Since all trials were conducted at the same distance (1 m) from the barrier position, only current barrier and pre-treatment were included as fixed factors. The addition of date as random intercept (L = 1.245, df = 1, P = 0.265) and slope (L < 0.001, df = 5, P = 1.000) did not significantly improve the fit of the model. Hence, the data were analysed using 2-way ANOVA. Pre-treatment had a significant main effect on the number of stings per trial ($F_{2,9}$ = 8.667, P = 0.008), however current barrier did not ($F_{2,9}$ = 2.167, P = 0.171) and there was no significant interaction ($F_{4,9}$ = 1.667, P = 0.241). The number of stings per trial was lower when the bees were pre-treated to either lattice (0.33 ± 0.33; P = 0.036) or hedge (0.00 ± 0.00; P = 0.008) compared to no barrier (1.33 ± 0.33), i.e. a reduction of 87% (Fig. 12.5).

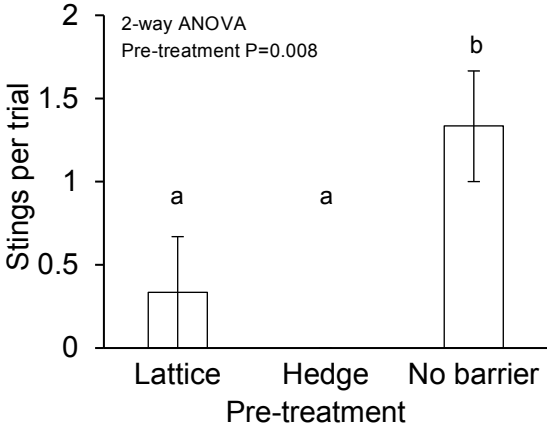


Figure 12.5. The effects of pre-treatment barrier on the number of stings per trial. Letters above bars represent the results of Tukey's *post-hoc* pairwise comparison tests. Bar heights are means ± standard error.

Discussion

The results show that a barrier always tended to raise honey bee flight height provided that it had been in place for a few days (i.e., was a pre-treatment). When the barrier treatment was changed, there was usually no immediate effect on flight height. The fact that a barrier needs to be in place for several days to be effective is not a problem for beekeepers, as barriers, whether hedges, lattice, or a building, are effectively permanent structures. However, it does lead to interesting questions in terms of honey bee memory and navigation. Returning foragers use special 'proximal' navigation in the hive vicinity, within a few metres, which is distinct from the 'distal' navigation used at long distances (Palikij *et al.*, 2012). Presumably, forager bees adopt a landing and take-off flight path that is appropriate to the barrier and use this path for some time even if the barrier is changed. This would indicate that they store multiple landmarks in their memory, so that changing one landmark, the presence or absence of a barrier, does not immediately change the flight path.

The effects on flight height were weak and inconsistent, probably because even in the absence of a barrier honey bees flew relatively high, mean c. 1.6 - 2.0 m. The effect of a 2 m barrier was, therefore, small, raising mean flight height to only c. 2.2 - 2.5 m. We deliberately used barriers of only 2 m as this is above the height of almost all humans (United States Census Bureau (2012) data show that 99.5-100% of men, depending on age group, and 100% of women are under 6 foot 6 inches tall (2m = 6 foot 6 ¾ inches)). In

addition, this is a convenient height both in the purchase of fencing materials (which are often 6 foot or just under 2 m, and so can be made 2 m high by raising slightly off the ground when attaching to support posts) and in hedge trimming. Furthermore, British planning regulations require boundary fences or walls of over 2 m in height to have special planning permission (http://www.planningportal.gov.uk/permission/commonprojects/fenceswallsgates). A beekeeper with an apiary in his or her garden can, therefore, erect a 2 m boundary fence without permission, except along road frontage where the maximum height is 1 m. Hedges are not restricted.

Our data indicate that barriers can potentially greatly reduce the chance of being stung in the vicinity of an apiary. This is of importance, as stinging is by far the most unwelcome thing that honey bees can do to people. Although experienced beekeepers are generally used to bee stings, members of the general public are not and a bee sting is generally a painful experience (Schmidt, 1990). Reduced stinging is probably a consequence of the greater proportion of forager bees flying above human height. However, the marked differences in sting rate between the two study apiaries suggest that the selection of non-aggressive colonies can also be of high importance. Colonies used in the Wakehurst apiary were loaned by a local semi-commercial bee-keeper, who had deliberately provided us with non-aggressive colonies for public safety reasons. In contrast, in the Plumpton apiary, colonies were randomly selected from those belonging to the Laboratory of Apiculture & Social Insects without regard to aggressiveness.

We think that these results would apply equally or possibly more strongly to solid barriers than to permeable ones, such as those used in this study. Casual observations made during the study and previous experience in using barriers around apiaries showed us that the vast majority of bees (> 95%) did not fly through the gaps in the barriers, but instead flew above them. This is similar to solid barriers, which do not allow any bees to fly through them. However, there are other considerations under which the use of an open barrier may be preferred. For example, depending on the layout of the apiary, open barriers may allow the hives to receive more direct sunshine and may promote better air circulation.

We conclude that barriers, such as those used in this study, are an effective way of reducing stings and contacts with bees in the vicinity of an apiary. We, therefore, recommend their use around apiaries, particularly in urban or suburban locations, such as private gardens or allotments, where nuisance to other people is likely to be a problem. Barriers are low cost and have other advantages, such as in reducing exposure to wind and improving security. Barriers may be of additional value when seeking permission to locate an apiary on borrowed land, such as on an allotment owned by a local council. The use of barriers could be considered an element of good practice, and one of several things that a beekeeper can do to reduce nuisance, and especially stinging, to other people.

Part 6: Final Discussion, References and Appendices

Chapter 13

Final Discussion

Under the wide umbrella of helping honey bees and other flower-visiting insects in urban areas, this thesis makes contributions in four distinct areas of research: (i) insect foraging on ornamental garden flowers (Chapters 3-7) and (ii) urban wild flowers (Chapters 8-9), (iii) urban honey bee foraging at the colony level (Chapters 10-11) and (iv) urban beekeeping (Chapter 12).

13.1 Insect foraging on urban garden flowers

One clear message from the research in this thesis is that the value of ornamental flowers to flower-visiting insects could be considerably improved and at no cost. The survey of the Southover Grange garden in Lewes showed that most plant varieties (61 of 79, 77%) being grown there were poorly attractive or completely unattractive to flower-visiting insects (Chapter 6). Although it is premature to draw general conclusions with respect to other gardens and parks, it is reasonable to suppose that the result found in Southover Grange is not unusual, given the popularity of certain plants with the public and the gardeners. For example, geraniums (*Pelargonium* spp. and varieties) are among the most popular bedding plants in Britain, yet are almost invariably unattractive to flower-visiting insects (Chapters 5, 6 and pers. obs.). Similarly, Frankie *et al.* (2005) found that in two Californian cities only about 13% of flowering ornamental plant species and varieties were attractive to flower-visiting insects to any measurable extent. However, not all is bad news. Chapters 5-7 showed that since popular and widely available garden plants vary enormously in their attractiveness to insect flower visitors, some judicious plant selection by gardeners can, potentially, make a big difference.

But how can we find out which plants are good for bees and other insect flower visitors? One way is to look up the advice in the numerous lists of recommended garden plants. However, as argued in Chapter 3, the recommendations there generally suffer from many shortcomings, such as being based on their author's personal experience and opinion. A better way is to rely on empirical data, such as that collected in the purpose-planted experimental garden on the University of Sussex campus (Chapter 5). But, the number of plant varieties studied in these experiments is necessarily rather low due to resource and time limitations. An alternative and less labour-intensive approach is to study plants that are already being grown in public parks or gardens (e.g. Chapter 6) or, indeed, national collections (Chapter 7). Chapter 4 provides a reassuring message that even plants growing in patches of different area can be compared without bias.

Furthermore, the methodology used to quantify plant attractiveness to flower-visiting insects in Chapters 5-7 should be sufficiently accessible to amateur enthusiasts and, therefore, could be used in 'citizen science' projects on a larger scale in the future. Indeed, there is at least one case where the methodology has already been taken up by one plant nursery, *rosybee*, specializing in bee-friendly plants, to run trials comparing attractiveness of plants to pollinators [http://www.rosybee.com/objectives], following its owner's attendance of a workshop in LASI.

13.2 Insect foraging on urban wild flowers

In urban areas, flower-visiting insects can benefit not only from garden ornamentals, but also from wild flowers that grow in the green spaces, such as public parks (Chapter 9), and, in the case of climbers like ivy, also on trees, building walls, fences and hedges (Chapter 8). Appreciating their value to beneficial flower-visiting insects, such as bees and butterflies, should help to promote the management practices that aim to encourage urban wildlife and biodiversity. Chapter 9 shows that a reduction in grass mowing intensity in an urban park caused a large increase in the abundance of both wild flower

blooms and flower-visiting insects, and that this practice was approved of by most park visitors, most of whom were local residents. Similarly, while common ivy is often blamed for damaging buildings and trees, it is the most important floral resource in late season for honey bees and other insects (Chapter 8), so appreciation of these benefits should hopefully have an impact on management decisions.

Future research directions in this area might include identification of other important floral resources for insects and ways to encourage them in urban areas. One obvious category of amenity plants widely planted in urban areas are trees. Some trees are already known for being important sources of nectar and pollen for honey bees. For example, the small-leaved lime tree, *Tilia cordata*, can provide up to c. 500 kg/ha of honey or more over a season (Crane, 1976). But the same may not be generally true of other lime species. The silver lime, *Tilia tomentosa*, for instance, has a nectar that is toxic to bees, particularly bumble bees, and it is not uncommon to find a number of dead bees on the ground below these trees during their flowering period (Crane, 1978; Pawlikowski, 2010). Trees, however, are challenging subjects to study due to their sheer size and the flowers being a large distance from the ground in the crown, which often makes them unreachable without special tools and equipment, such as an elevating work platform.

13.3 Urban honey bee foraging at the colony level

Interestingly, Chapter 10 found that honey bee colonies located in Brighton, UK, foraged almost exclusively in the surrounding urban area year round. This suggests that there was a sufficient amount of floral resources to support them. Throughout the season, the bees rarely ventured into the surrounding countryside, and were not tempted even by the dense monocultures of spring flowering oilseed rape (Chapter 11), although it was well within their reach, as bees can forage at distances of up to c. 10-12 km (Beekman & Ratnieks, 2000). Indeed, on average, the foraging distances of urban hives were lower than those of the rural hives on the University of Sussex campus (Couvillon *et al.*, 2014a),

suggesting that the urban area may be richer in floral resources than the nearby rural area. However, analysis of foraging preferences in the rural hives alone showed that urban areas were not, on average, preferred significantly more or less than other types of landscape, while indicating both a significant preference and a significant aversion of lands managed under certain agri-environment schemes (Couvillon *et al.*, 2014b). But, studies such as these inevitably have an element of local idiosyncrasy and it remains to be seen whether these results are general with respect to other towns and cities in the UK and elsewhere.

13.4 Urban beekeeping

This thesis includes only one chapter addressing an aspect of urban beekeeping. Chapter 12 shows that using a barrier, such as a fence or a hedge, around an apiary can be considered good practice in urban beekeeping, as it tends to increase bee flight height and, probably as a consequence, reduce the chance of being stung for people nearby. However, people will, perhaps, never be completely safe from stings in the vicinity of an apiary. Honey bee colonies are known to be very variable in their aggressiveness and, indeed, the information presented in Chapter 12 suggests that colony choice may play an important role. To further increase human safety, honey bee breeders could select colonies for, among other desirable traits, a lesser inclination of workers to sting.

13.5 Final remarks

Human population is growing at a high rate. United Nations (2013) estimates show that by the year 2050 there could be between 8.6 and 10.9 billion humans on our planet. At the same time, natural habitats are being put under an ever increasing amount of pressure due to extraction of resources or to make way for development and agriculture. Perhaps, one day, urban and agricultural landscapes will be the dominant types of landscape in many areas of the world. This is already the case in the present-day Britain, and especially

England, which is amongst the most densely populated areas in Europe. Thus, in this respect, it may represent a kind of a 'climax' landscape. It is, therefore, not surprising that the global biodiversity is experiencing a decline on par with the five great mass extinction events in the history of the Earth, when over 75% of all species have gone extinct in a geologically short period of time (Barnosky *et al.*, 2011). It would be naïve to suppose that we could restore the Earth's biodiversity close to its pre-industrial levels or at least preserve it in its present state, even if human population growth is halted today. However, what we can do is make our environment, as much as possible, friendly to wildlife, and learn to co-exist with what is left of it. This thesis is a tiny contribution to knowledge in this important and massive endeavour.

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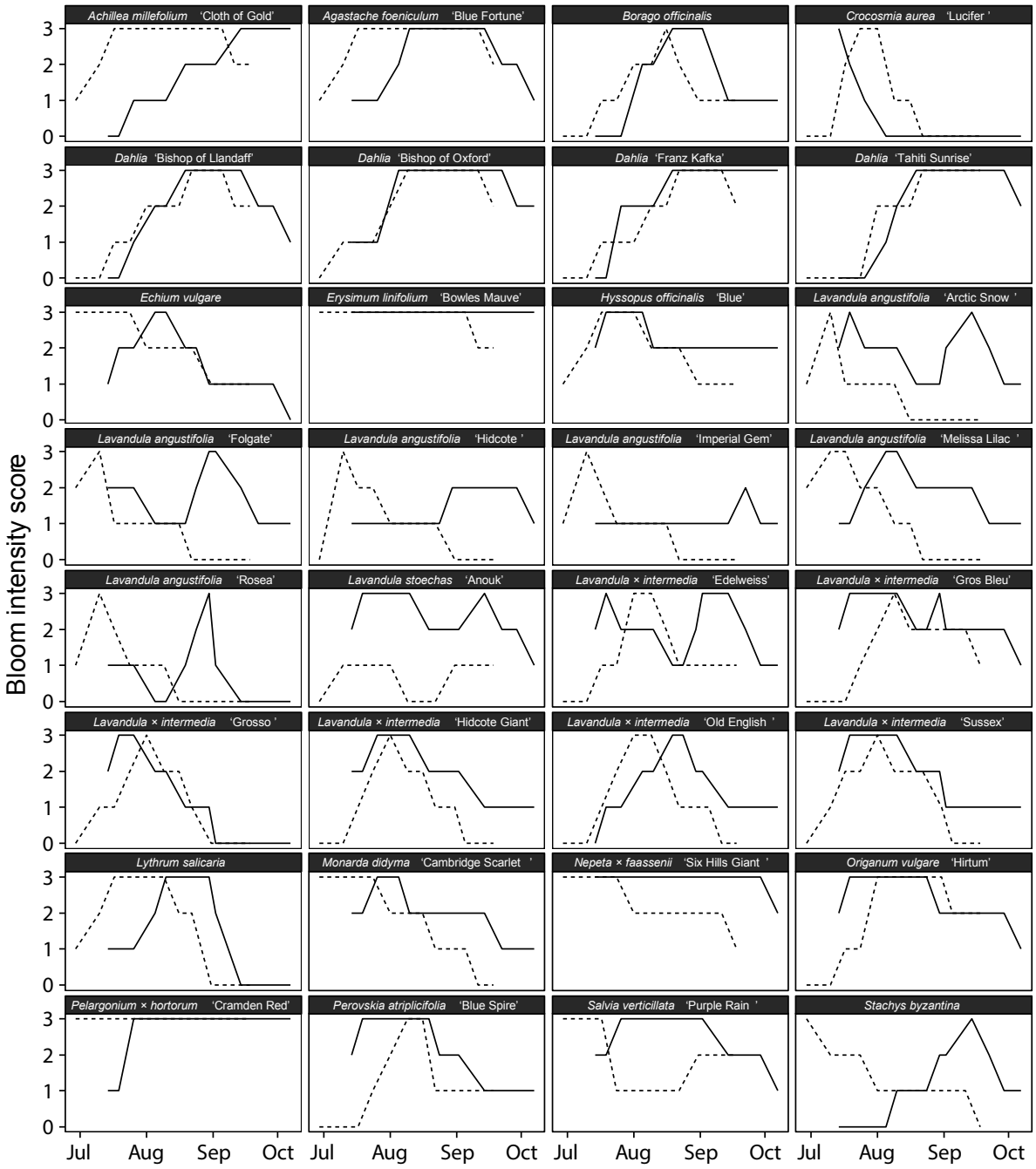
Appendix 5.1. List of plant varieties used in the study, arranged in alphabetic order

#	Scientific name	Common name	Plant variety	Native to Britain?	Plants per m²	Supplier
1	*Achillea millefolium*	Yarrow	Cloth of Gold	Native	16	Burncoose Nurseries
2	*Agastache foeniculum*	Anise Hyssop	Blue Fortune	Exotic	9	Coblands Nurseries
3	*Borago officinalis**	Borage	Wildtype	Exotic	9	Thompson & Morgan
4	*Crocosmia aurea*	Crocosmia	Lucifer	Exotic	16	Birchfield Nursery
5	*Dahlia × hortensis**	Dahlia	Bishop of Llandaff (open flower)	Exotic	9	J Parker's Dutch Bulbs
6	*Dahlia** (hybrid, unknown parentage)	Dahlia	Bishop of Oxford (open flower)	Exotic	9	J Parker's Dutch Bulbs
7	*Dahlia** (hybrid, unknown parentage)	Dahlia	Franz Kafka (ball/pompom)	Exotic	9	J Parker's Dutch Bulbs
8	*Dahlia** (hybrid, unknown parentage)	Dahlia	Tahiti Sunrise (semi-cactus)	Exotic	9	J Parker's Dutch Bulbs
9	*Echium vulgare*	Viper's Bugloss	Wildtype	Native	16	Larch Cottage Nurseries
10	*Erysimum linifolium**	Perennial Wallflower	Bowles Mauve	Exotic	16	Burncoose Nurseries
11	*Hyssopus officinalis*	Hyssop	Blue	Exotic	16	The Beth Chatto Gardens
12	*Lavandula angustifolia**	English Lavender	Arctic White	Exotic	9	Downderry Nursery
13	*Lavandula angustifolia*	English Lavender	Folgate	Exotic	9	Downderry Nursery
14	*Lavandula angustifolia*	English Lavender	Hidcote	Exotic	9	Downderry Nursery
15	*Lavandula angustifolia*	English Lavender	Imperial Gem	Exotic	9	Downderry Nursery
16	*Lavandula angustifolia**	English Lavender	Melissa Lilac	Exotic	9	Downderry Nursery
17	*Lavandula angustifolia*	English Lavender	Rosea	Exotic	9	Downderry Nursery
18	*Lavandula stoechas*	French Lavender	Anouk	Exotic	9	B & Q
19	*Lavandula x intermedia**	Lavandin	Edelweiss	Exotic	9	Downderry Nursery
20	*Lavandula x intermedia*	Lavandin	Gros Bleu	Exotic	9	Downderry Nursery
21	*Lavandula x intermedia**	Lavandin	Grosso	Exotic	9	Downderry Nursery
22	*Lavandula x intermedia*	Lavandin	Hidcote Giant	Exotic	9	Downderry Nursery
23	*Lavandula x intermedia*	Lavandin	Old English	Exotic	9	Downderry Nursery
24	*Lavandula x intermedia*	Lavandin	Sussex	Exotic	9	Downderry Nursery
25	*Lythrum salicaria*	Purple Loosestrife	Wildtype	Native	9	Knoll Gardens
26	*Monarda didyma*	Bergamot, Bee Balm	Cambridge Scarlet	Exotic	16	Burncoose Nurseries
27	*Nepeta × faassenii*	Catmint	Six Hills Giant	Exotic	9	Burncoose Nurseries
28	*Origanum vulgare**	Greek Origanum	Hirtum	Native	16	National Herb Centre
29	*Pelargonium x hortorum**	Geranium	Cramden Red	Exotic	9	Fibrex Nurseries
30	*Perovskia atriplicifolia*	Russian Sage	Blue Spire	Exotic	9	Coblands Nurseries
31	*Salvia verticillata*	Lilac Sage	Purple Rain	Exotic	16	Birchfield Nursery
32	*Stachys byzantina*	Lamb's Ear	Wildtype	Exotic	16	Binny Plants

* Variety replicated in two additional locations in 2012

Appendix 5.2. Bloom intensity scores of the 32 plant varieties planted on the University of Sussex campus in 2011 (solid line) and 2012 (dashed line). The beginning and the end of each line show the first and the last day of data collection in each year.

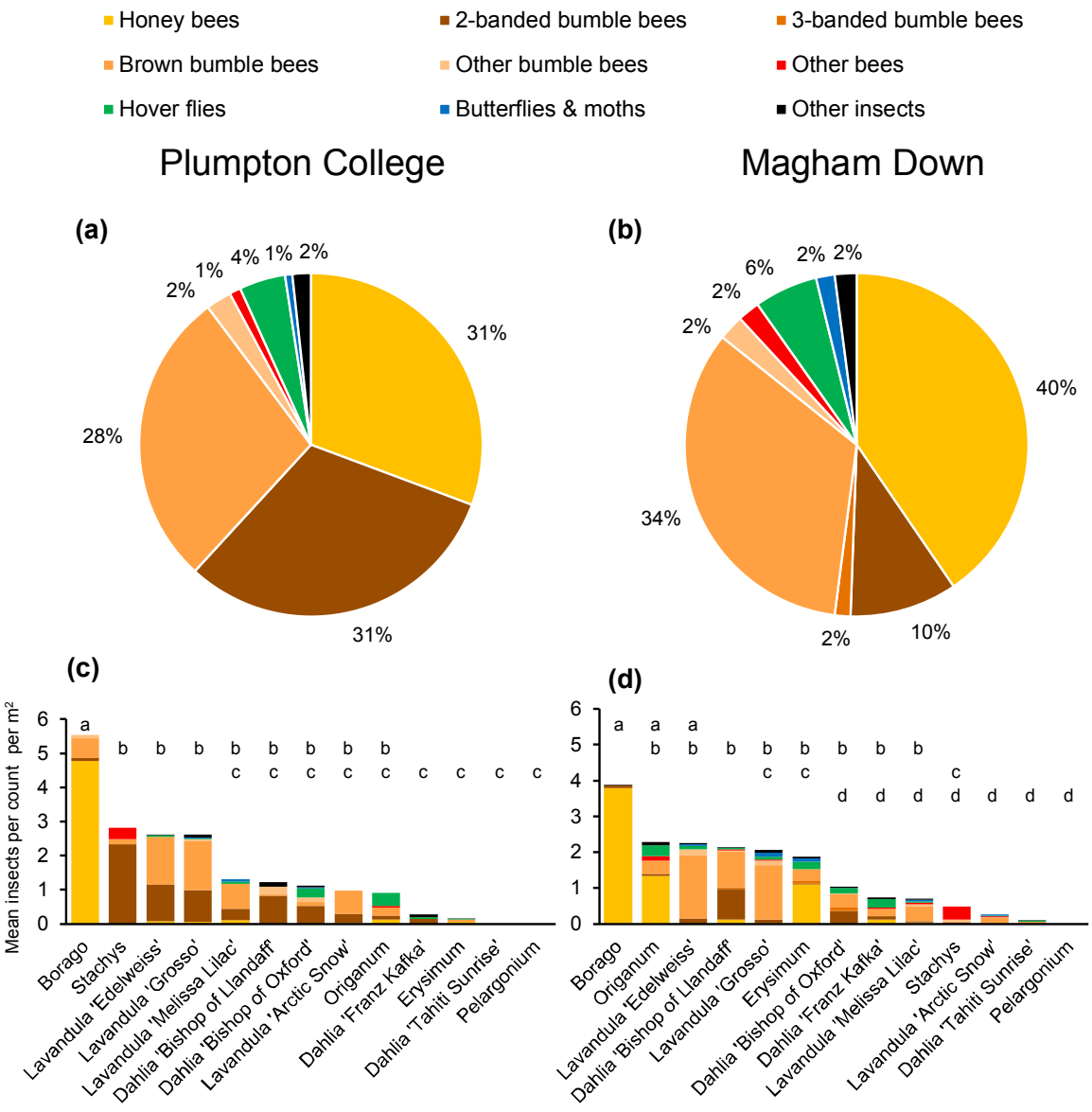


Appendix 5.3. P-values of factors affecting the daily average number of insects per m^2 of each insect group in a series of GLMs

	University of Sussex 2011			University of Sussex 2012			Plumpton College 2012		Magham Down 2012	
Insect group	**Bloom intensity**	**Plant variety**	**Corolla length**	**Bloom intensity**	**Plant variety**	**Corolla length**	**Bloom intensity**	**Plant variety**	**Bloom intensity**	**Plant variety**
1. *Apis mellifera*	F=64.89	F=8.73	F=16.33	F=94.86	F=5.61	F=5.37	F=0.22	F=14.01	F=0.92	F=17.67
	df=1	df=31	df=1 b=-0.04	df=1	df=31	df=1 b=-0.03	df=1	df=12	df=1	df=12
	P<0.001	**P<0.001**	**P<0.001**	**P<0.001**	**P<0.001**	P=0.021	P=0.640	**P<0.001**	P=0.339	**P<0.001**
2. *Bombus terrestris/lucorum*	F=137.28	F=10.00	F=1.44	F=109.81	F=6.40	F=5.42	F=5.72	F=6.29	F=7.09	F=9.59
	df=1	df=31	df=1 b=-0.01	df=1	df=31	df=1 b=-0.02	df=1	df=12	df=1	df=12
	P<0.001	**P<0.001**	P=0.231	**P<0.001**	**P<0.001**	P=0.021	P=0.020	**P<0.001**	P=0.009	**P<0.001**
3. *Bombus hortorum*	F=26.89	F=4.00	F=1.78	F=36.42	F=7.68	F=5.58	None recorded		F=5.01	F=2.30
	df=1	df=31	df=1 b=-0.001	df=1	df=31	df=1 b=0.004	-		df=1	df=12
	P<0.001	**P<0.001**	P=0.183	**P<0.001**	**P<0.001**	P=0.019	-		P=0.028	P=0.013
4. *Bombus pascuorum*	F=6.84	F=6.95	F<0.01	F=16.45	F=6.32	F=0.16	F=2.78	F=6.03	F=1.68	F=6.59
	df=1	df=31	df=1 b=$2x10^{-4}$	df=1	df=31	df=1 b=-0.003	df=1	df=12	df=1	df=12
	P=0.009	**P<0.001**	P=0.963	**P<0.001**	**P<0.001**	P=0.686	P=0.100	**P<0.001**	P=0.194	**P<0.001**
5. Other *Bombus* spp.	F=32.68	F=4.87	F=2.48	F=32.28	F=6.55	F=14.04	F=5.40	F=2.14	F=0.51	F=1.96
	df=1	df=31	df=1 b=-0.002	df=1	df=31	df=1 b=-0.008	df=1	df=12	df=1	df=12
	P<0.001	**P<0.001**	P=0.116	**P<0.001**	**P<0.001**	**P<0.001**	P=0.023	P=0.026	P=0.479	P=0.037
6. Other bees	F=1.01	F=3.83	F=0.02	F=8.19	F=4.76	F=5.10	F=0.95	F=1.05	F=0.03	F=3.93
	df=1	df=31	df=1 b=$6x10^{-4}$	df=1	df=31	df=1 b=0.01	df=1	df=12	df=1	df=12
	P=0.315	**P<0.001**	P=0.875	**P=0.005**	**P<0.001**	P=0.025	P=0.334	P=0.417	P=0.868	**P<0.001**
7. Dipetera: Syrphidae	F=4.82	F=4.37	F=2.69	F=40.53	F=7.23	F=8.80	F=0.25	F=1.63	F=2.06	F=2.72
	df=1	df=31	df=1 b=0.009	df=1	df=31	df=1 b=-0.02	df=1	df=12	df=1	df=12
	P=0.029	**P<0.001**	P=0.102	**P<0.001**	**P<0.001**	**P=0.003**	P=0.615	P=0.105	P=0.154	**P=0.004**
8. Lepidoptera	F=25.25	F=3.73	F=0.01	F=53.31	F=3.72	F=5.89	Too few recorded, n=7		F=0.09	F=1.10
	df=1	df=31	df=1 b=$6x10^{-5}$	df=1	df=31	df=1 b=-0.004	-		df=1	df=12
	P<0.001	**P<0.001**	P=0.904	**P<0.001**	**P<0.001**	P=0.016	-		P=0.759	P=0.370
9. Other insects	F<0.01	F=1.04	F=0.59	F=29.76	F=14.11	F=18.71	F=1.03	F=1.10	Too few recorded, n=1	
	df=1	df=31	df=1 b=$-4x10^{-4}$	df=1	df=31	df=1 b=-0.01	df=1	df=12	-	
	P=0.924	P=0.414	P=0.441	**P<0.001**	**P<0.001**	**P<0.001**	P=0.314	P=0.379	-	

P-values in bold are significant at α=0.05 after Bonferroni correction.

Appendix 5.4. Relative abundance of insects in 9 main groups recorded at Plumpton College (a) and Magham Down (b) in 2012 and their corresponding daily means per count per 1×1 m patch recorded on 13 garden plant varieties (c,d). Letters above bars represent significant differences based on Tukey's HSD test, where varieties sharing a common letter are not significantly different from each other at α=0.05. More detailed taxonomic breakdowns of other bumble bees, other bees, butterflies+moths, and other insects are given in Table 5.1 and full plant names in Appendix 5.1.



Appendix 6.1. Seventy-nine plant varieties surveyed in the Southover Grange garden.

Broad category		Plant species / variety	Insects per count per m^2	Total area (m^2)
Highly attractive	1	*Sedum* (unidentified, green-leaved)	14.34	2.0
	2	*Sedum* (unidentified, red-leaved)	12.84	0.7
	3	*Origanum vulgare*	11.24	1.9
Moderately attractive	4	*Xerochrysum* 'Florabella Gold'	4.56	1.2
	5	*Salvia* 'Mystic Spires Blue'	3.75	1.0
	6	*Coleus* 'Dark Chocolate'	3.62	0.4
	7	*Cynara cardunculus*	2.07	9.4
	8	*Echinops sphaerocephalus*	2.02	6.2
	9	*Astrantia* sp.	1.78	1.1
	10	Unidentified	1.78	0.5
	11	*Dahlia* 'Bishop of York'	1.77	1.1
	12	*Lythrum salicaria*	1.59	1.1
	13	*Dahlia* 'Esther'	1.34	1.3
	14	*Erysimum linifolium* 'Bowles' Mauve'	1.33	0.6
	15	*Rudbeckia laciniata* 'Herbstsonne'	1.33	1.2
	16	*Althaea* sp.	1.22	2.0
	17	*Cosmos sonata* (unidentified, white)	1.14	0.4
	18	*Sanvitalia* 'Golden Aztec'	1.10	1.8
Poorly attractive	19	*Echinops ritro*	0.78	2.6
	20	*Cosmos sonata* (unidentified, light pink)	0.67	2.1
	21	*Dahlia* 'Bishop of Llandaff'	0.66	3.2
	22	*Salvia* 'Victoria Blue'	0.60	14.6
	23	*Nepeta* sp.	0.59	1.4
	24	*Achillea millefolium*	0.57	2.2
	25	*Gazania* 'Daybreak'	0.56	0.2
	26	*Cosmos sonata* (unidentified, dark pink)	0.52	1.9
	27	*Echinacea purpurea*	0.44	0.2
	28	*Matricaria* 'White Stars'	0.40	1.7
	29	*Anchusa azurea* 'Loddon Royalist'	0.39	1.5
	30	*Lavatera trimestris* 'Rose Beauty'	0.27	2.3
	31	Unidentified	0.25	1.8
	32	*Salvia* 'Victoria White'	0.25	25.5
	33	*Verbena bonariensis*	0.23	5.4
	34	*Nicotiana sylvestris* 'Only the Lonely'	0.21	0.6
	35	*Calendula officinalis* 'Fiesta Gitana'	0.20	0.7
	36	*Dahlia* 'David Howard'	0.14	6.1
	37	*Helenium* sp.	0.11	3.1
	38	*Dahlia* 'Rosella'	0.10	4.7
	39	*Helianthus* 'Bronze'	0.10	2.0
	40	*Dahlia* 'Impression Festivo'	0.10	1.4

Appendix 6.1. Continued.

	41	*Anemone hupehensis japonica* 'Pamina'	0.08	5.2
	42	*Dahlia* 'Glory of Noordwyk'	0.08	2.6
	43	*Canna* (unidentified, green-leaved)	0.07	3.0
	44	*Argyranthemum madeira* 'Primrose'	0.06	17.5
	45	*Crocosmia* sp.	0.06	1.1
	46	*Fuchsia* sp.	0.06	1.2
	47	*Physostegia virginiana*	0.06	1.2
	48	*Canna* (unidentified, dark-leaved)	0.06	3.6
	49	*Cleome spinosa*	0.05	2.8
	50	*Dahlia* 'Arabian Night'	0.05	1.4
	51	*Abutilon pictum* 'Thompsonii'	0.04	1.8
	52	*Acanthus dioscoridis*	0.03	9.8
	53	*Abutilon* 'Savitzii'	0.02	16.3
	54	*Pelargonium* 'Maverick White'	0.02	4.3
	55	*Petunia* 'Wave Blue'	0.01	19.2
Completely unattractive	56	*Agapanthus* sp.	0.00	1.0
	57	*Alchemilla* sp.	0.00	5.4
	58	*Argyranthemum madeira* 'Crested Merlot'	0.00	22.0
	59	*Aster* 'Starlight'	0.00	1.5
	60	*Begonia* 'Heaven White'	0.00	4.5
	61	*Canna* (unidentified, mixed)	0.00	1.0
	62	*Celosia* 'Century Mix'	0.00	0.9
	63	*Cleome odysee* (mixed varieties)	0.00	5.0
	64	*Dahlia* 'Babylon Paars'	0.00	4.7
	65	*Dahlia* 'Barbarossa'	0.00	1.2
	66	*Dahlia* 'My Love'	0.00	2.6
	67	*Eutrochium purpureum*	0.00	14.3
	68	*Impatiens* 'New Guinea'	0.00	0.3
	69	*Nicotiana affinis*	0.00	11.2
	70	*Osteospermum* 'Oriana Terracotta'	0.00	0.3
	71	*Pelargonium* 'Maverick Coral'	0.00	18.6
	72	*Pelargonium* 'Maverick Red'	0.00	40.7
	73	*Pelargonium* (unidentified, pink)	0.00	6.2
	74	*Phlox* sp.	0.00	0.9
	75	*Phygelius* × *rectus* 'Winchester Fanfare'	0.00	0.6
	76	*Rudbeckia* 'Marmalade'	0.00	0.4
	77	*Rudbeckia fulgida* 'Goldsturm'	0.00	0.5
	78	*Salvia* 'Strata'	0.00	0.8
	79	*Verbena* 'Aztec Coral'	0.00	1.1

Appendix 7.1. Attractiveness of 228 *Aster* varieties to flower-visiting insects, as surveyed in the UK National Collection, along with their attributes, including attributes relevant to gardening. Varieties are arranged in descending order of their attractiveness to all insects. Highlighted in yellow and green are the 12 and 25 most attractive varieties to honey bees and hover flies, respectively, attracting >2 insects per m^2, on average, over the monitoring period, as shown in Figure 7.4a,b.

Species	Variety	Insects per count per m^2			Weighted bloom intensity score			Attributes relevant to gardening			Floral traits	
		Honey bees	Hover flies	All insects	Visit 1 (14-15 Sep)	Visit 2 (28-29 Sep)	Visit 3 (19-20 Oct)	Attractiveness to humans	Ease of cultivation	Availability in UK	Main colour	Capitulum size (cm^2)
A. novi-belgii	Alice Haslam	8.12	6.64	15.20	3.0	2.0	0.0	Medium	Intermediate	Very common	Pink	11.2
A. novi-belgii	Alderman Vokes	3.33	7.78	11.48	2.0	2.0	1.0	Medium	Intermediate	Very rare	Pink	19.2
A. novi-belgii	Dandy	6.88	2.29	10.07	3.0	1.0	0.0	Medium	Intermediate	Common	Pink	7.9
A. novi-belgii	Little Man in Blue	2.93	4.84	7.82	2.0	3.0	2.0	High	Specialist	Rare	Blue	9.6
A. novi-belgii	Anneke	2.68	4.43	7.27	3.0	1.5	0.0	Medium	Intermediate	Rare	Pink	7.5
A. novi-belgii	Hilda Ballard	4.54	2.59	7.22	3.0	3.0	0.0	Medium	Intermediate	Very rare	Purple	18.1
A. amellus	King George	0.07	5.63	6.32	3.0	2.6	0.9	High	Specialist	Very common	Purple	27.3
A. novi-belgii	Boningale White	2.83	2.93	5.86	3.0	2.0	0.0	Medium	Intermediate	Rare	White	14.1
A. novi-belgii	Marries Pretty Please	2.20	3.10	5.47	2.6	1.4	1.4	Low	Specialist	Very rare	Purple	9.9
A. amellus	Sternkugel	0.08	4.95	5.41	2.9	3.0	1.2	Medium	Easy	Rare	Blue	30.7
A. amellus	Mrs. Ralph Woods	0.24	4.54	5.36	2.6	2.4	0.0	Medium	Intermediate	Very rare	Pink	20.7
A. amellus	Vanity	0.33	4.59	5.33	3.0	2.0	1.0	High	Specialist	Rare	Blue	27.5
A. novi-belgii	King of Belgians	0.98	3.82	5.24	3.0	3.0	1.0	High	Specialist	Very rare	Blue	14.4
A. ericoides x cordifolius	Prairie Pink	1.70	3.22	5.19	3.0	2.0	1.0	Medium	Specialist	Very rare	Pink	4.9
A. novi-belgii	Blue Lagoon	1.94	3.15	5.09	3.0	3.0	0.0	Medium	Specialist	Common	Blue	16.3
A. novi-belgii	Lisa Dawn	2.00	2.97	5.03	3.0	2.0	0.0	High	Intermediate	Rare	Pink	12.6
A. novi-belgii	Royal Ruby	3.10	1.50	4.73	2.2	2.4	0.0	High	Intermediate	Rare	Pink	16.0
A. novae-angliae	Little Alma	2.93	0.82	4.42	2.0	2.0	0.0	Medium	Specialist	Very rare	Pink	11.6
A. novi-belgii	Faith	0.83	3.49	4.38	2.0	2.0	0.0	High	Intermediate	Very rare	Purple	17.8
A. novi-belgii	Norman's Jubilee	1.06	2.98	4.15	3.0	1.5	0.0	High	Intermediate	Rare	Pink	16.2
A. novi-belgii	Mistress Quickly	2.59	1.36	4.08	3.0	2.0	1.0	Medium	Intermediate	Rare	Purple	14.3
A. novi-belgii	Elsie Dale	0.73	3.33	4.06	3.0	3.0	0.0	Medium	Intermediate	Very rare	Pink	11.2
A. amellus	Nocturne	0.00	3.11	3.86	2.0	3.0	1.3	High	Intermediate	Rare	Purple	28.5
A. novi-belgii	Melbourne Belle	1.87	1.87	3.73	2.0	2.0	0.0	Medium	Intermediate	Very rare	Pink	23.6
A. novi-belgii	Jenny	2.34	1.24	3.67	2.4	2.3	0.0	High	Intermediate	Very common	Pink	10.7
A. cordifolius x laevis	Prairie Purple	1.28	2.08	3.50	3.0	2.0	2.0	High	Specialist	Rare	Purple	8.6

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Species	Variety	Insects per count per m^2			Weighted bloom intensity score			Attributes relevant to gardening			Floral traits	
		Honey bees	Hover flies	All insects	Visit 1 (14-15 Sep)	Visit 2 (28-29 Sep)	Visit 3 (19-20 Oct)	Attractiveness to humans	Ease of cultivation	Availability in UK	Main colour	Capitulum size (cm^2)
A. amellus	Jaqueline Genebrier	0.00	3.49	3.49	2.0	2.0	2.0	High	Intermediate	Rare	Pink	10.9
A. salignus	Prairie Pearl	0.80	2.00	3.33	2.0	3.0	1.0	High	Specialist	Very rare	Purple	7.7
A. novae-angliae	Barr's Pink	1.33	1.38	3.32	1.6	2.4	1.2	High	Specialist	Very common	Pink	24.2
A. novi-belgii	Tovarich	1.85	1.31	3.27	3.0	2.0	0.0	High	Intermediate	Rare	Blue	7.5
A. novae-angliae	Little Bella	1.53	1.39	3.22	2.0	2.0	0.0	Medium	Specialist	Very rare	Pink	17.3
A. novi-belgii	Patricia Ballard	1.62	1.28	2.99	3.0	2.0	0.0	Medium	Intermediate	Very common	Pink	12.3
A. novae-angliae	Treasure	1.33	0.80	2.76	2.0	3.0	2.0	Medium	Specialist	Rare	Blue	14.4
A. novi-belgii	Ada Ballard	1.02	1.50	2.65	3.0	2.0	0.0	High	Intermediate	Very common	Blue	22.9
A. novi-belgii	Eventide	0.36	1.60	2.58	1.0	3.0	1.0	Medium	Easy	Rare	Purple	23.8
A. amellus	Brilliant	0.00	2.47	2.54	2.7	2.7	1.0	High	Intermediate	Very common	Purple	16.7
A. novae-angliae	Violetta	1.39	0.37	2.49	2.0	2.0	0.0	High	Specialist	Common	Purple	20.6
A. novi-belgii	Richness	1.71	0.68	2.46	2.0	3.0	1.0	Medium	Intermediate	Very rare	Pink	9.0
A. novae-angliae	Pale Violetta	0.48	1.32	2.41	2.0	3.0	1.0	Medium	Specialist	Very rare	Pink	18.2
A. amellus	Sonia	0.00	1.92	2.40	1.7	3.0	0.7	Medium	Intermediate	Rare	Pink	24.1
A. novae-angliae	Helen Picton	1.75	0.08	2.36	1.0	2.0	0.0	High	Specialist	Common	Purple	15.6
A. novae-angliae	Mrs. S. T. Wright	0.88	1.21	2.35	2.0	3.0	1.0	High	Specialist	Common	Purple	29.4
A. spectabilis	Wildtype	0.09	2.13	2.31	3.0	3.0	0.0	Low	Easy	Rare	Blue	11.3
A. novi-belgii	Autumn Days	0.89	1.30	2.26	2.0	3.0	0.0	Medium	Intermediate	Very rare	Pink	27.7
Aster hybrid, unknown parentage	Prairie Violet	0.99	1.19	2.22	2.0	2.0	1.0	Low	Specialist	Very rare	Blue	12.3
A. amellus	Grunder	0.04	2.10	2.16	2.2	3.0	2.4	High	Intermediate	Rare	Blue	32.5
A. novae-angliae	Primrose Upward	1.25	0.76	2.15	1.0	2.0	0.0	High	Specialist	Rare	Pink	15.3
A. novi-belgii	Sarah Ballard	1.16	0.95	2.12	1.0	2.0	1.0	High	Intermediate	Very rare	Purple	22.4
A x frikartii	Eiger	0.00	2.00	2.11	3.0	3.0	2.0	Medium	Intermediate	Very rare	Blue	26.8
A. novi-belgii	Peter Chiswell	0.97	1.03	2.05	2.0	3.0	0.0	High	Intermediate	Rare	Pink	8.9
A x frikartii	Wunder von Staffa	0.00	1.89	1.96	3.0	2.3	1.9	High	Specialist	Very common	Purple	25.4
A. novae-angliae	Brunswick	0.73	1.01	1.94	1.5	2.5	1.5	Medium	Specialist	Very rare	Purple	14.6
A. novi-belgii	Autumn Beauty	0.10	1.57	1.92	2.0	3.0	0.0	High	Intermediate	Very rare	Purple	22.4
A. novi-belgii	Elizabeth Hutton	0.18	1.73	1.90	2.0	2.0	1.0	Medium	Intermediate	Very rare	Pink	15.1
A. novi-belgii	Saint Egwin	0.23	1.47	1.87	1.0	3.0	1.0	Medium	Specialist	Very rare	Pink	3.9

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Species	Variety	Insects per count per m^2			Weighted bloom intensity score			Attributes relevant to gardening			Floral traits	
		Honey bees	Hover flies	All insects	Visit 1 (14-15 Sep)	Visit 2 (28-29 Sep)	Visit 3 (19-20 Oct)	Attractiveness to humans	Ease of cultivation	Availability in UK	Main colour	Capitulum size (cm^2)
A. novi-belgii	Lassie	0.56	0.97	1.76	2.0	3.0	1.0	High	Specialist	Rare	Pink	17.9
A. novi-belgii	Snowsprite	0.85	0.79	1.75	2.0	3.0	1.0	High	Intermediate	Rare	White	10.5
A. novi-belgii	Irene	0.96	0.52	1.73	0.6	3.0	2.4	Medium	Intermediate	Very rare	Pink	12.4
A. novae-angliae	Purple Paradise	0.57	0.78	1.62	3.0	2.0	1.0	Medium	Specialist	Very rare	Purple	16.9
A. ageratoides	Forncett Flourish	0.08	1.23	1.56	1.0	2.0	3.0	High	Intermediate	Rare	Blue	16.6
A. novi-belgii	Trudi Ann	0.07	1.46	1.53	2.0	3.0	0.0	High	Intermediate	Rare	Purple	11.7
A. novi-belgii	Erica	0.00	1.30	1.48	1.0	3.0	1.0	Medium	Intermediate	Rare	Pink	15.6
A x frikartii	Mönch	0.01	1.38	1.43	2.9	2.1	1.3	High	Specialist	Very common	Purple	17.6
A. novi-belgii	Anita Ballard	0.30	0.95	1.42	2.0	3.0	0.0	High	Intermediate	Very rare	Blue	14.5
A. novi-belgii	Heinz Richard	0.95	0.32	1.38	0.0	2.0	1.0	High	Intermediate	Common	Pink	8.0
A. novi-belgii	Destiny	0.56	0.67	1.33	1.0	3.0	2.0	Low	Intermediate	Very rare	Purple	21.4
A. novae-angliae	Ladies Days	0.87	0.35	1.30	2.0	2.0	0.0	Medium	Specialist	Very rare	Pink	11.2
A. novi-belgii	Anita Webb	0.25	0.91	1.26	2.6	2.4	0.0	High	Intermediate	Very rare	Pink	10.4
A. novi-belgii	Blue Boy	0.24	0.88	1.22	1.6	3.0	1.0	Medium	Intermediate	Rare	Blue	7.0
A. ericoides	Wildtype	0.00	1.05	1.22	1.6	3.0	0.0	Medium	Specialist	Common	White	0.9
A. cordifolius hybrid	Little Carlow	0.61	0.52	1.16	1.0	2.0	1.4	High	Specialist	Very common	Blue	5.3
A. novi-belgii	Little Pink Lady	0.20	0.79	1.12	1.0	3.0	1.0	Medium	Intermediate	Rare	Pink	8.4
A. amellus	Kobold	0.00	0.93	1.11	2.0	3.0	1.0	High	Easy	Very rare	Purple	13.1
A. novi-belgii	Freda Ballard	0.32	0.70	1.07	3.0	2.5	0.5	Medium	Intermediate	Common	Pink	14.5
A. pyrenaeus	Lutetia	0.00	1.05	1.07	3.0	2.2	1.6	High	Specialist	Very common	Purple	14.8
A. cordifolius	Chieftain	0.37	0.59	1.03	1.0	3.0	0.0	High	Intermediate	Rare	Blue	2.8
A. novi-belgii	Saphire	0.34	0.61	1.02	1.3	2.3	2.0	Medium	Intermediate	Common	Purple	9.6
A. novi-belgii	Dolly	0.11	0.83	1.00	2.0	3.0	0.0	Medium	Intermediate	Rare	Pink	12.2
A. novi-belgii	Blue Radiance	0.56	0.44	1.00	1.0	3.0	2.0	High	Easy	Very rare	Blue	38.9
A. novi-belgii	Little Pink Beauty	0.48	0.47	1.00	0.0	3.0	0.0	High	Specialist	Very common	Pink	5.5
A. trinervius ssp. *figeratoides*	Asran	0.06	0.86	0.97	1.4	3.0	3.0	Medium	Specialist	Very rare	Purple	8.8
A. novi-belgii	School Girl	0.36	0.48	0.95	1.0	3.0	1.0	High	Easy	Very rare	Pink	21.2
A. novi-belgii	Christine Soanes	0.33	0.56	0.94	1.0	3.0	1.0	Medium	Intermediate	Very rare	Pink	21.1
A. novi-belgii	Little Red Boy	0.11	0.68	0.91	2.0	3.0	0.0	Low	Easy	Very rare	Pink	9.3
A. asperulus	Wildtype	0.00	0.88	0.88	2.0	2.0	2.0	High	Specialist	Rare	Blue	16.2

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Species	Variety	Insects per count per m^2			Weighted bloom intensity score			Attributes relevant to gardening			Floral traits	
		Honey bees	Hover flies	All insects	Visit 1 (14-15 Sep)	Visit 2 (28-29 Sep)	Visit 3 (19-20 Oct)	Attractiveness to humans	Ease of cultivation	Availability in UK	Main colour	Capitulum size (cm^2)
A. novi-belgii	Madge Cato	0.40	0.47	0.87	2.0	3.0	2.0	High	Intermediate	Rare	Purple	22.1
A. novae-angliae	Colwall Galaxy	0.11	0.42	0.85	1.0	2.0	1.0	Medium	Specialist	Rare	Pink	17.5
A. novi-belgii	Fair Lady	0.21	0.32	0.85	1.0	2.0	2.0	Medium	Intermediate	Rare	Pink	12.6
A. novi-belgii	Albanian	0.07	0.62	0.84	1.0	3.0	0.5	High	Intermediate	Very rare	White	13.9
A. novi-belgii	The Bishop	0.03	0.74	0.81	0.5	2.3	0.0	Medium	Easy	Very rare	Purple	14.3
A. novi-belgii	Apollo	0.08	0.54	0.78	1.0	2.0	2.0	High	Intermediate	Rare	White	10.3
A. amellus	Sonora	0.00	0.76	0.76	2.0	2.4	0.4	High	Intermediate	Rare	Purple	21.2
A x frikartii	Jung Frau	0.00	0.74	0.74	2.0	2.0	3.0	High	Specialist	Common	Blue	20.7
A. novi-belgii	Coombe Margaret	0.07	0.67	0.74	0.0	1.0	2.0	High	Intermediate	Very rare	Pink	15.5
A. novi-belgii	Gayborder Royal	0.37	0.29	0.73	2.0	3.0	1.0	Medium	Intermediate	Rare	Purple	4.6
A. novi-belgii	Blauglut	0.27	0.43	0.72	1.6	3.0	2.0	High	Specialist	Very rare	Purple	14.5
A. cordifolius	Elegans	0.14	0.57	0.71	1.0	3.0	3.0	High	Intermediate	Rare	White	1.2
A. novi-belgii	Mount Everest	0.45	0.26	0.71	0.0	3.0	1.0	High	Intermediate	Rare	White	18.7
A. novi-belgii	Gurney Slade	0.42	0.17	0.67	0.0	2.0	3.0	High	Intermediate	Very rare	Purple	11.3
A. laevis	Arcturus	0.14	0.46	0.65	1.0	3.0	2.0	Medium	Specialist	Rare	Purple	13.2
A. novae-angliae	Herbstchnee	0.13	0.51	0.63	1.0	1.0	2.0	High	Specialist	Very common	White	13.1
A. novi-belgii	Waterperry	0.00	0.34	0.62	1.0	3.0	1.0	High	Intermediate	Rare	Pink	14.7
A. novae-angliae	Augusta	0.40	0.18	0.60	2.2	3.0	1.0	High	Specialist	Rare	Purple	16.0
A. novi-belgii	Steine Bruck	0.26	0.26	0.59	0.0	1.0	3.0	High	Intermediate	Very rare	White	6.4
A. cordifolius hybrid	Alderboran	0.10	0.35	0.48	0.9	1.9	2.0	Medium	Easy	Rare	White	1.2
A. novi-belgii	Sandford's White Swa	0.06	0.36	0.48	2.0	3.0	0.0	High	Intermediate	Rare	White	17.9
A. oblongifolius	Wildtype	0.02	0.43	0.47	1.6	2.0	1.0	Medium	Intermediate	Rare	Purple	9.1
Aster hybrid, unknown parentage	Les Moutiers	0.00	0.13	0.45	1.0	2.0	3.0	Medium	Specialist	Very rare	Purple	5.1
A. novae-angliae	Pink Parfait	0.00	0.00	0.44	0.0	3.0	1.0	Medium	Specialist	Common	Pink	5.4
A. novi-belgii	Dora Chiswell	0.00	0.44	0.44	2.1	3.0	0.4	Medium	Intermediate	Very rare	Purple	8.6
A. novi-belgii	Elta	0.00	0.43	0.43	0.7	2.0	2.0	Medium	Specialist	Very rare	Pink	11.4
A. novi-belgii	Rosenwitchel	0.28	0.07	0.42	0.5	1.0	1.0	High	Intermediate	Rare	Pink	6.2
A. novi-belgii	Helen Ballard	0.30	0.12	0.42	1.0	3.0	2.0	High	Intermediate	Rare	Pink	13.7
A. amellus	Morehein Gem	0.00	0.41	0.41	1.4	2.6	1.0	High	Intermediate	Rare	Blue	22.9
A. novi-belgii	Coombe Rosemary	0.10	0.20	0.40	1.0	3.0	0.0	Medium	Intermediate	Rare	Purple	14.1

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Species	Variety	Insects per count per m^2			Weighted bloom intensity score			Attributes relevant to gardening			Floral traits	
		Honey bees	Hover flies	All insects	Visit 1 (14-15 Sep)	Visit 2 (28-29 Sep)	Visit 3 (19-20 Oct)	Attractiveness to humans	Ease of cultivation	Availability in UK	Main colour	Capitulum size (cm^2)
A. lateriflorus hybrid	Coombe Fishacre	0.00	0.39	0.39	1.0	3.0	1.0	High	Specialist	Very common	Purple	4.4
A. ageratoides	Stardust	0.00	0.32	0.35	1.0	2.0	2.4	Medium	Specialist	Very rare	White	6.0
A. novi-belgii	Apple Blossom	0.17	0.17	0.34	1.0	2.0	2.0	High	Easy	Very rare	Purple	19.3
A. novi-belgii	Chequers	0.00	0.33	0.33	2.0	3.0	0.0	High	Specialist	Rare	Purple	12.6
A. novi-belgii	Melbourne Magnet	0.00	0.11	0.33	0.0	1.0	3.0	High	Intermediate	Very rare	Purple	15.6
A. novi-belgii	Little Boy Blue	0.06	0.19	0.32	1.0	2.0	1.0	Medium	Intermediate	Rare	Blue	10.6
A. novae-angliae	Lucida	0.10	0.21	0.31	1.0	1.0	1.0	High	Specialist	Rare	Pink	12.6
A. laevis	Vesta	0.04	0.10	0.31	0.0	0.7	3.0	High	Specialist	Rare	White	10.0
A. novi-belgii	Fellowship	0.09	0.13	0.31	0.0	2.0	3.0	High	Intermediate	Very common	Pink	11.8
A. novi-belgii	Cameo	0.00	0.30	0.30	0.0	2.0	1.0	Low	Intermediate	Very rare	Pink	10.2
A. novae-angliae	Quinton Menzies	0.10	0.10	0.30	1.0	2.0	0.0	High	Specialist	Rare	Pink	13.9
A. novi-belgii	Schneekissen	0.00	0.24	0.30	1.0	2.0	1.0	Medium	Intermediate	Very rare	White	6.7
A. novi-belgii	Cecily	0.08	0.12	0.29	0.4	2.4	2.0	High	Specialist	Rare	Purple	8.7
A. novi-belgii	Victor	0.00	0.29	0.29	0.0	1.0	1.0	High	Intermediate	Very rare	Purple	7.5
A. novi-belgii	Chatterbox	0.06	0.23	0.28	2.0	3.0	0.0	High	Specialist	Common	Pink	12.9
A. novi-belgii	Freya	0.09	0.13	0.26	0.0	3.0	1.0	High	Intermediate	Rare	Pink	21.6
A. novi-belgii	Eva	0.00	0.00	0.26	0.0	2.0	2.0	Medium	Intermediate	Rare	Pink	8.9
A. novi-belgii	Lavender Dream	0.00	0.26	0.26	1.0	3.0	2.0	Medium	Intermediate	Very rare	Pink	18.9
A. novi-belgii	Schone von Dietlikon	0.04	0.08	0.25	0.0	2.0	3.0	High	Intermediate	Very rare	Purple	6.6
A. novi-belgii	Terry's Pride	0.00	0.05	0.25	0.0	1.0	2.0	High	Intermediate	Rare	Pink	13.3
A. novi-belgii	Marie Ballard	0.00	0.25	0.25	3.0	3.0	1.0	High	Intermediate	Very common	Purple	12.6
A. novae-angliae	Purple Dome	0.00	0.19	0.23	0.9	0.9	0.0	High	Intermediate	Common	Purple	11.9
A. novi-belgii	Grey Lady	0.00	0.23	0.23	0.0	1.0	3.0	Medium	Specialist	Very rare	Purple	7.2
A. novi-belgii	Cantab	0.11	0.11	0.22	0.0	1.0	3.0	Medium	Intermediate	Very rare	Purple	4.7
A. novi-belgii	Dazzler	0.06	0.11	0.22	0.0	1.0	2.0	Medium	Intermediate	Rare	Pink	7.4
A. novi-belgii	Marie Ann Niel	0.00	0.11	0.22	0.0	1.0	3.0	Medium	Intermediate	Rare	Purple	8.9
A. novi-belgii	Blue Moon	0.00	0.00	0.22	0.0	0.0	3.0	High	Specialist	Very rare	Blue	6.9
A. novi-belgii	Pride of Colwall	0.05	0.10	0.21	1.0	3.0	2.0	High	Intermediate	Rare	Pink	8.2
A. amellus	Framfieldii	0.00	0.21	0.21	0.6	1.6	1.2	Medium	Intermediate	Rare	Purple	6.6
A. novi-belgii	Janet Watts	0.07	0.14	0.20	2.0	3.0	1.0	High	Intermediate	Very rare	Pink	19.5

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Species	Variety	Insects per count per m^2			Weighted bloom intensity score			Attributes relevant to gardening			Floral traits	
		Honey bees	Hover flies	All insects	Visit 1 (14-15 Sep)	Visit 2 (28-29 Sep)	Visit 3 (19-20 Oct)	Attractiveness to humans	Ease of cultivation	Availability in UK	Main colour	Capitulum size (cm^2)
A. lateriflorus	Horizontalis cv. Prince	0.00	0.15	0.20	0.0	1.0	2.0	High	Specialist	Very common	White	1.4
A. pyrenaeus x amellus	Cotswold Gem	0.00	0.10	0.19	1.0	2.0	3.0	High	Specialist	Rare	Purple	12.8
A. novi-belgii	Guardsman	0.19	0.00	0.19	0.0	2.0	0.0	Medium	Intermediate	Very rare	Pink	7.6
A. novi-belgii	Dusky Maid	0.00	0.09	0.19	0.0	2.0	3.0	High	Intermediate	Rare	Pink	22.7
A. novi-belgii	Algar's Pride	0.06	0.12	0.18	0.0	1.0	3.0	High	Intermediate	Rare	Purple	34.2
A. novi-belgii	Coombe Gladys	0.09	0.09	0.17	0.0	2.0	1.0	Medium	Intermediate	Very rare	Pink	17.1
A. novi-belgii	Royal Velvet	0.00	0.00	0.17	0.0	0.0	3.0	Medium	Intermediate	Very rare	Purple	8.2
A. novi-belgii	Remembrance	0.00	0.08	0.16	0.0	0.0	2.0	High	Intermediate	Rare	Purple	10.3
A. novi-belgii	Pamela	0.16	0.00	0.16	3.0	2.0	0.0	Medium	Intermediate	Very rare	Pink	16.0
A. novi-belgii	Timsbury	0.00	0.07	0.14	0.0	2.0	2.0	High	Intermediate	Rare	Pink	15.5
A. novi-belgii	Jean	0.00	0.00	0.14	0.0	1.0	3.0	Medium	Intermediate	Rare	Purple	9.5
A. amellus	Rosa Erfullung	0.00	0.11	0.13	1.2	1.2	2.6	High	Intermediate	Very common	Pink	16.0
Aster hybrid, unknown parentage	Octoberlicht	0.00	0.03	0.13	0.0	1.0	3.0	High	Specialist	Rare	White	11.6
A. ericoides	Cinderella	0.00	0.13	0.13	0.0	1.0	3.0	Medium	Intermediate	Rare	White	1.2
A. novi-belgii	Beechwood Charm	0.00	0.13	0.13	0.0	0.0	3.0	High	Specialist	Very rare	Pink	5.6
A. novi-belgii	Ralph Picton	0.00	0.06	0.13	0.0	1.0	3.0	Medium	Intermediate	Very rare	Pink	14.5
A. novi-belgii	Blue Bouquet	0.00	0.00	0.13	0.0	1.0	3.0	Medium	Intermediate	Rare	Blue	9.6
A. novi-belgii	Niobe	0.00	0.12	0.12	0.0	0.0	1.0	Low	Intermediate	Very rare	White	3.1
A. novi-belgii	Blue Eyes	0.03	0.07	0.12	1.8	3.0	1.8	High	Intermediate	Very rare	Blue	8.3
A. novae-angliae	Anabelle de Chazal	0.02	0.10	0.11	0.6	1.4	1.0	High	Specialist	Rare	Pink	11.7
A. novi-belgii	Harrison's Blue	0.00	0.11	0.11	0.0	1.0	3.0	Medium	Intermediate	Rare	Purple	18.4
A. novi-belgii	Blue Spire	0.00	0.00	0.11	0.0	0.0	3.0	Medium	Intermediate	Very rare	Purple	5.1
A. amellus	Violet Queen	0.00	0.11	0.11	0.5	1.3	2.3	High	Easy	Very common	Purple	16.2
A. novi-belgii	Cliff Lewis	0.00	0.10	0.10	0.6	2.0	1.0	Medium	Intermediate	Very rare	Purple	15.7
A. novi-belgii	Dietgard	0.03	0.07	0.10	0.0	0.0	1.5	High	Intermediate	Rare	Pink	3.7
A. amellus	Rudolph Goethe	0.00	0.09	0.09	2.0	3.0	2.0	High	Specialist	Common	Purple	21.2
A. novi-belgii	Lady Frances	0.00	0.09	0.09	2.0	3.0	0.0	High	Intermediate	Rare	Pink	15.5
A. pringlei	Phoebe	0.00	0.00	0.08	0.0	0.0	3.0	High	Specialist	Rare	Purple	6.9
A. cordifolius	Silver Spray	0.00	0.08	0.08	1.0	3.0	2.0	High	Specialist	Common	White	1.1

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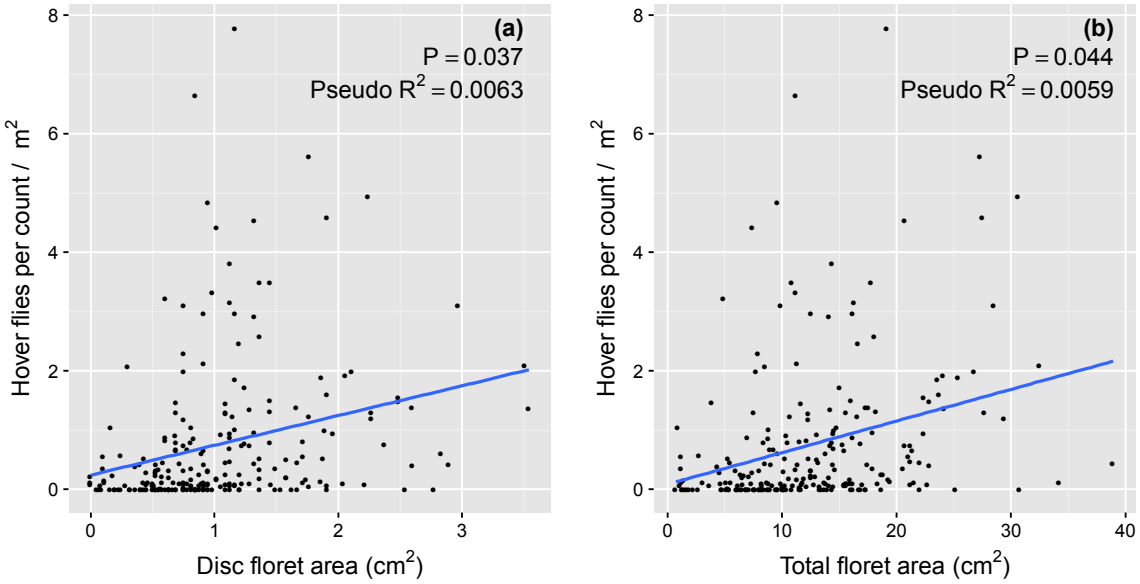
		Honey bees	Hover flies	All insects	Visit 1 (14-15 Sep)	Visit 2 (28-29 Sep)	Visit 3 (19-20 Oct)	Attractiveness to humans	Ease of cultivation	Availability in UK	Main colour	Capitulum size (cm^2)
A. novi-belgii	Blande	0.00	0.08	0.08	0.0	1.0	2.0	High	Intermediate	Rare	White	9.2
A. novi-belgii	Carlingcot	0.00	0.07	0.07	0.0	2.0	2.0	Medium	Intermediate	Very rare	Purple	11.0
A. novi-belgii	Daniella	0.00	0.00	0.07	0.0	1.0	1.0	High	Intermediate	Rare	Pink	8.0
A. laevis	Calliope	0.00	0.07	0.07	0.0	1.0	3.0	High	Specialist	Very common	Purple	14.2
A. novi-belgii	Winston Churchill	0.07	0.00	0.07	0.0	3.0	0.0	High	Intermediate	Common	Pink	8.0
A. novi-belgii	Beauty of Colwall	0.00	0.00	0.07	0.0	1.0	3.0	Medium	Intermediate	Very rare	Purple	10.1
A. novi-belgii	Daur Blau	0.00	0.00	0.06	0.0	1.0	3.0	Low	Specialist	Very rare	Blue	10.9
A. novi-belgii	Thundercloud	0.06	0.00	0.06	0.0	1.0	3.0	High	Intermediate	Rare	Pink	13.3
A. novi-belgii	Porzellan	0.00	0.00	0.06	0.0	0.0	2.0	Medium	Intermediate	Common	Purple	13.5
A. novi-belgii	Autumn Rose	0.00	0.05	0.05	0.0	0.0	1.0	Medium	Intermediate	Very rare	Pink	12.2
A. novi-belgii	Sam Bantam	0.00	0.04	0.04	0.0	1.6	2.0	High	Specialist	Very rare	White	10.1
A. novi-belgii	Sophia	0.00	0.02	0.02	0.0	2.0	1.8	High	Intermediate	Common	Pink	5.3
Aster hybrid, unknown parentage	Diamond Jubilee	0.00	0.00	0.02	0.0	0.0	1.0	High	Specialist	Very rare	White	4.8
A. novi-belgii	Baby Climax	0.00	0.01	0.01	0.0	0.0	2.0	Medium	Specialist	Very rare	Purple	6.2
A. amellus	Weltfriede	0.00	0.00	0.00	0.0	2.0	3.0	Medium	Easy	Rare	Blue	18.7
A. cordifolius	Photograph	0.00	0.00	0.00	0.0	0.0	2.0	High	Intermediate	Common	Blue	1.9
A. ericoides	Esther	0.00	0.00	0.00	0.0	1.0	1.0	High	Easy	Rare	Purple	2.7
A. ericoides	forma prostratus Snow Flurry	0.00	0.00	0.00	0.0	0.0	2.0	High	Specialist	Very common	White	0.7
A. ericoides hybrid	Blue Star	0.00	0.00	0.00	0.0	0.0	2.5	High	Specialist	Common	Blue	1.6
A. ericoides hybrid	Golden Spray	0.00	0.00	0.00	0.0	0.0	0.5	High	Intermediate	Common	White	1.3
A. lateriflorus	Bleke Bet	0.00	0.00	0.00	0.0	0.0	1.0	Medium	Easy	Rare	White	2.3
A. lateriflorus	Bucks Fizz	0.00	0.00	0.00	0.0	1.0	2.5	Medium	Specialist	Rare	White	1.7
A. lateriflorus	Horizontalis	0.00	0.00	0.00	0.0	0.0	3.0	High	Specialist	Very common	Pink	1.4
A. novae-angliae	Colwall Century	0.00	0.00	0.00	0.0	0.0	2.0	High	Specialist	Rare	Pink	9.0
A. novae-angliae	Colwall Orbit	0.00	0.00	0.00	1.0	3.0	1.0	Medium	Intermediate	Rare	Pink	7.2
A. novae-angliae	Evensong	0.00	0.00	0.00	0.0	0.0	1.0	Medium	Specialist	Rare	Pink	8.8
A. novae-angliae	Harrington's Pink	0.00	0.00	0.00	0.0	0.0	0.0	Medium	Specialist	Very common	Pink	10.2
A. novae-angliae	Naomi	0.00	0.00	0.00	0.0	1.0	2.0	Medium	Specialist	Rare	Pink	9.7
A. novae-angliae	Rubinschatz	0.00	0.00	0.00	0.0	1.0	2.0	Medium	Specialist	Rare	Pink	14.0
A. novi-belgii	Autumn Glory	0.00	0.00	0.00	0.0	1.0	3.0	High	Easy	Very rare	Pink	30.8

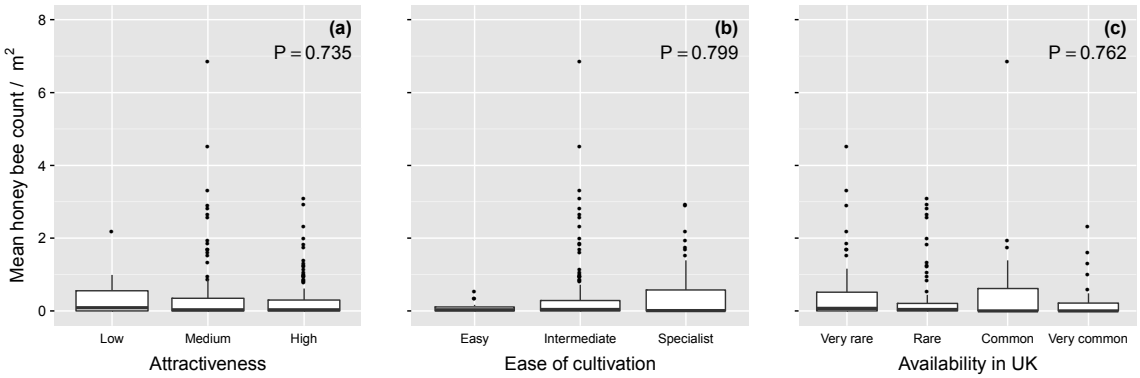
Continued on next page…

Species	Variety	Insects per count per m^2			Weighted bloom intensity score			Attributes relevant to gardening			Floral traits	
		Honey bees	Hover flies	All insects	Visit 1 (14-15 Sep)	Visit 2 (28-29 Sep)	Visit 3 (19-20 Oct)	Attractiveness to humans	Ease of cultivation	Availability in UK	Main colour	Capitulum size (cm^2)
A. novi-belgii	Beechwood Challenger	0.00	0.00	0.00	0.0	0.0	3.0	High	Intermediate	Rare	Pink	7.0
A. novi-belgii	Brightest & Best	0.00	0.00	0.00	0.0	2.0	0.0	Medium	Easy	Very rare	Pink	16.9
A. novi-belgii	Charles Wilson	0.00	0.00	0.00	0.0	0.0	3.0	Medium	Intermediate	Rare	Pink	8.2
A. novi-belgii	Coombe Radiance	0.00	0.00	0.00	0.0	0.0	2.0	High	Intermediate	Very rare	Pink	14.4
A. novi-belgii	Davy's True Blue	0.00	0.00	0.00	0.0	1.0	3.0	High	Intermediate	Rare	Purple	16.2
A. novi-belgii	Feckenham Rival	0.00	0.00	0.00	1.0	3.0	1.0	Medium	Specialist	Very rare	Pink	11.7
A. novi-belgii	Fuldatal	0.00	0.00	0.00	0.0	1.0	3.0	High	Intermediate	Very rare	Pink	25.2
A. novi-belgii	Gulliver	0.00	0.00	0.00	0.0	0.0	3.0	High	Intermediate	Rare	Pink	10.2
A. novi-belgii	Guy Ballard	0.00	0.00	0.00	0.0	0.0	2.0	Medium	Intermediate	Very rare	Pink	13.7
A. novi-belgii	Jeanette	0.00	0.00	0.00	0.0	0.0	3.0	Medium	Intermediate	Rare	Purple	6.5
A. novi-belgii	Kassel	0.00	0.00	0.00	0.0	0.0	0.0	High	Intermediate	Rare	Pink	5.4
A. novi-belgii	Kristina	0.00	0.00	0.00	0.0	0.0	1.0	Medium	Intermediate	Common	White	6.1
A. novi-belgii	Lady in Blue	0.00	0.00	0.00	0.0	1.0	0.0	High	Specialist	Very common	Purple	6.1
A. novi-belgii	Margery Bennett	0.00	0.00	0.00	2.0	2.0	2.0	Medium	Intermediate	Very rare	Pink	11.6
A. novi-belgii	Mary Dean	0.00	0.00	0.00	0.0	1.0	2.0	Medium	Easy	Very rare	Pink	16.8
A. novi-belgii	Midget	0.00	0.00	0.00	0.0	0.0	2.0	Low	Intermediate	Very rare	Blue	6.4
A. novi-belgii	Priory Blush	0.00	0.00	0.00	0.0	1.0	0.0	High	Intermediate	Rare	Pink	10.4
A. novi-belgii	Professor Anton von Kippenberg	0.00	0.00	0.00	0.0	1.0	2.4	High	Intermediate	Common	Purple	7.7
A. novi-belgii	Rose Bonnet	0.00	0.00	0.00	0.0	0.0	2.0	High	Intermediate	Rare	Pink	4.8
A. novi-belgii	Rosebud	0.00	0.00	0.00	1.0	2.0	0.0	Medium	Intermediate	Very rare	Pink	8.4
A. novi-belgii	Rufus	0.00	0.00	0.00	0.0	2.0	2.0	High	Intermediate	Very rare	Pink	17.3
A. novi-belgii	Sheena	0.00	0.00	0.00	0.0	2.0	0.0	High	Intermediate	Rare	Pink	22.1
A. novi-belgii	White Wings	0.00	0.00	0.00	1.0	1.0	2.0	High	Intermediate	Rare	White	17.3
A. pringlei	Ochtendgloren	0.00	0.00	0.00	0.0	0.0	2.0	High	Specialist	Very common	Pink	7.5

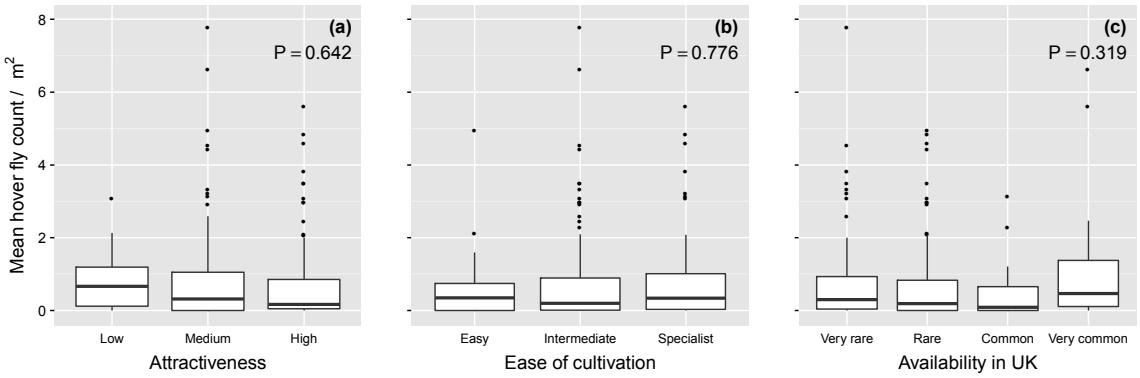
Appendix 7.2. Relationships of hover fly flower visitation with (a) disc floret area and (b) total capitulum area. The relationships are significant only prior to Bonferroni-correction for multiple models (α = 0.05 / 2 = 0.025). Pseudo R^2 values for models fit by maximum likelihood with generalized least squares method are calculated using the McFadden's formula (Veall & Zimmermann, 1996).



Appendix 7.3. Associations of honey bee visitation with variety attributes relevant to gardening: (a) attractiveness to humans, (b) ease of cultivation and (c) availability in UK.



Appendix 7.4. Associations of hover fly visitation with variety attributes relevant to gardening: (a) attractiveness to humans, (b) ease of cultivation and (c) availability in UK.



Appendix 9.1. Total numbers of flowering units counted across the whole project period (18/06/2013 - 18/09/2013) in the Saltdean Oval park

	Treatment				Flowering unit definition
	Regular mowing	Mowing until July	Mowing until June	No mowing	
Lotus corniculatus	7669	8430	10947	30266	Flower
Pimpinella saxifraga	1309	3914	5585	9084	Compound umbel
Centaurea nigra	1209	9622	7968	8771	Capitulum
Ononis repens	509	700	2103	8685	Flower
Thymus polytrichus	6677	6717	2904	8139	Raceme
Hypochaeris radicata	6910	10232	10039	7889	Capitulum
Daucus carota	4242	6463	6187	6183	Compound umbel
Galium verum	213	1758	3770	5571	Panicle
Trifolium pratense	895	1363	2246	5063	Umbel
Crepis capillaris	2444	2549	2840	4408	Capitulum
Galium mollugo	101	160	1224	4405	Panicle
Trifolium repens	917	1251	1959	2567	Umbel
Cerastium fontanum	92	147	510	2296	Flower
Achillea millefolium	48	1092	2195	2098	Corymb
Senecio jacobaea	0	47	535	1846	Capitulum
Convolvulus arvensis	548	1742	1147	1159	Flower
Medicago lupulina	1686	720	394	864	Raceme
Ranunculus bulbosus	63	181	663	678	Flower
Linum catharticum	178	252	234	336	Flower
Prunella vulgaris	221	195	207	328	Verticillaster
Sherardia arvensis	35	6	37	266	Cyme
Bellis perennis	275	243	380	234	Capitulum
Trifolium fragiferum	2	0	0	110	Umbel
Knautia arvensis	0	14	10	99	Capitulum
Centaurea scabiosa	1	24	27	90	Capitulum
Cirsium acaule	79	51	30	70	Capitulum
Ranunculus sp.	0	0	0	65	Flower
Cirsium vulgare	0	5	0	23	Capitulum
Glechoma hederacea	0	0	0	11	Verticillaster
Trifolium medium	1	1	0	8	Umbeel
Ranunculus sardous	0	0	0	5	Flower
Odontites vernus	0	1	0	4	Raceme
Picris echioides	0	0	63	3	Capitulum
Agrimonia eupatoria	1	3	1	2	Spike
Geranium pusillum	0	0	6	1	Flower
Geranium sp.	1	0	4	1	Flower
Trifolium hybridum	0	0	0	1	Umbel
Asperula cynanchica	0	15	20	0	Compound cyme
Centaurea sp.	0	3	0	0	Capitulum
Ranunculus repens	0	13	0	0	Flower
Taraxacum sp.	1	2	2	0	Capitulum

*Species not in bold were not recorded being foraged on by any flower-visiting insects

Appendix 9.2. Questionnaire and summary of responses on the Saltdean Oval grass management

Total: 39 respondents

Status of respondents

Sex:	31% Male	69% Female

Age group:	5%	18-30
	24%	31-40
	14%	41-50
	11%	51-60
	19%	61-70
	27%	70+

Do you live near the Saltdean Oval park?	86% Yes	14% No
If yes, for how long have you lived there?	Average = 12.6 years	

How often do you visit the Saltdean Oval park?

11%	Rarely
9%	Less than once a month
20%	Once a week
60%	Almost every day

For what purpose do you usually visit the park?
(not mutually exclusive options)

42%	Relax
42%	Walk
63%	Walk the dog
45%	Take children to play
18%	Look at plants
21%	Look at insects
8%	Other

Attitudes towards park management and the environment

Have you noticed any changes to the management of the park?	61% Yes	31% No
Have you noticed the wildflowers in the long grass?	72% Yes	28% No
Have you noticed bees or butterflies?	79% Yes	21% No
Do you think it is a good idea to encourage insects and wildflowers?	97% Yes	3% No

Appendix 9.2. Continued.

Is the amount of long grass appropriate?	74% Yes	26% No

If no, is there too much or too little?

88%	Too much
11%	Too little

Has the long grass changed how you use the park?	23% Yes	77% No

If yes, how?

78%	Avoid long grass
22%	Have to be careful when walking the dog

Has the long grass changed how you enjoy the park?	36% Yes	64% No

If yes, how?

71%	Enjoy the park more due to more colour / flowers / butterflies
29%	Enjoy the park less / dislike long grass

Would you be interested in learning more about the bees, butterflies and other species that live in the long grass?	54% Yes	46% No

If yes, what kinds of things would you be interested in learning?
(not mutually exclusive options)

86%	Flowering plant identification
76%	Bee identification
91%	Butterfly identification
71%	Management of flower rich meadows
81%	Bee and butterfly conservation and reasons for decline
5%	Other

Would you be interested in helping to collect data about the species in the park?	38% Yes	62% No

Additional question with permission of taking a respondent to an experimental block
(Number of respondents who agreed = 16)

Looking at these four strips, which do you prefer?

69%	No mowing
31%	Mowing until July
13%	Mowing until June
13%	Regular mowing

Appendix 9.3. Tukey's post-hoc pairwise comparison tests among the four mowing treatments in blocks, following up on the three measures of plants or insects used in the three GLMs outlined in Table 9.1.

Pairwise comparison	Number of flowering units per m^2		Number of plant species in flower per strip		Mean number of insects on flowers per transect-walk in a strip	
	t-value	P-value	t-value	P-value	t-value	P-value
Regular mowing - Mowing until July	2.12	0.150	3.73	**0.002**	1.83	0.261
Regular mowing - Mowing until June	2.75	**0.033**	4.34	**<0.001**	3.44	**0.004**
Regular mowing - No mowing	7.41	**<0.001**	5.32	**<0.001**	6.06	**<0.001**
Mowing until July - Mowing until June	0.62	0.925	0.61	0.929	1.60	0.380
Mowing until July - No mowing	5.28	**<0.001**	1.59	0.385	4.23	**<0.001**
Mowing until June - No mowing	4.66	**<0.001**	0.98	0.759	2.62	**0.046**